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Catchability of American Lobsters (*Homarus americanus*) and Rock Crabs (*Cancer irroratus*) by Traps

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Miller, R. J. 1989. Catchability of american lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) by traps. Can. J. Fish. Aquat. Sci. 46: 1652–1657.

Catches per trap of lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) were compared to densities of each species measured by divers. Trapping and diver surveys were carried out in habitats with and without macroalgae. Catchability coefficients (catch per trap/animal density) increased greatly with animal size. For example, in a habitat with macroalgae catchabilities were 13, 47, and 492 $m^2 \cdot trap^{-1}$ for lobsters of 50–59, 60–69, and 70–89 mm carapace length, respectively. For crabs of 60–79 and ≥80 mm carapace width, catchabilities increased by factors of three or seven, depending on habitat type. Data from trap catches and diver surveys agreed that lobster, biomass was similar and size frequencies different between habitats. Trapping and diving results also agreed that crab biomass and size frequency differed between habitats.

On a comparé les captures de homards (*Homarus americanus*) et de crabes (*Cancer irroratus*) par casier à la densité de chaque espèce mesurée par des plongeurs. On a fait les captures et les relevés dans des habitats avec et sans macro-algues. On a constaté que le coefficient de capturabilité (captures par casier/densité d'animaux) augmentait considérablement en fonction de la grosseur de l'animal. Par exemple, dans un habitat avec macro-algues, la capturabilité des homards ayant une carapace de 50–59, 60–69 et 70–89 mm de longueur était respectivement de 13, 47, et 492 $m^2 \cdot casier^{-1}$. Quant aux crabes, la capturabilité de ceux dont la carapace mesurait 60–79 et 80 mm ou plus de largeur augmentait par un facteur de trois ou de sept, tout dépendant du type d'habitat étudié. On a constaté que les données de la pêche et des relevés indiquaient toutes deux que, pour les homards, la biomasse était semblable d'un habitat à l'autre, tandis que la fréquence des tailles différait. Quant aux crabes, les deux types de données indiquaient que, et la biomasse, et la fréquence des tailles différaient d'un habitat à l'autre.

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Many factors related to fishing gear, habitat, and biology of the target species influence catch rates of decapods by baited traps (Bennett and Brown 1979). Catch rate, c/f (in number of animals per trap), is related to absolute density, D (in animals per square metre), by the catchability coefficient, q (in square metres per trap).

$$c/f = qD$$

If a catchability coefficient is found to be a reliable calibration factor for a particular trap type, target species, and set of environmental conditions, it can then be used to convert catch per trap to animal density.

Similar formulations have been used by Chittleborough (1970); Morgan (1974); Miller (1975); Melville-Smith (1986); and Miller and Hunte (1987), although notation differed from the above. In the first two studies the unit area was a hectare, and in the last three catchability was termed "effective area fished." Note that q is smaller than the actual area from which the target animals are attracted to a trap. For these areas to be the same, 100% of the target animals must be captured from inside and none from outside the area. Almost certainly, a decreasing fraction would be captured at increasing distance downstream from a trap without a 100% probability of capture at any distance. Himmelman (1988) has shown this to be the case for a whelk.

In this study catchability coefficients were calculated from catch rates of different-sized American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*), in two habitat types. Lobster and crab densities were carefully measured by divers.

Methods

Study Area

Scuba divers recorded depth, substrate type, and plant cover at 49 stations in each of two adjacent habitat types at the entrance to Louisbourg Harbor (45°54.4′N, 50°48.0′W) off eastern Cape Breton Island, Nova Scotia. Both areas ranged from 3–9 m depth at mean low water and covered approximately 4800 m^2 of bottom. In the 'kelp habitat' macroalgae covered 30–100% of the bottom and averaged 70%. The overstory was kelp, *Laminaria longicruris*, and the understory either a red alga, *Chondrus crispus*, or any of a variety of filamentous algae. The substratum was small boulders and cobble set in sand and gravel. The 'barren habitat' located 75 m to the south at the closest point, averaged <5% algal cover, all filamentous species. The substratum was somewhat coarser, with a few large protruding boulders, but mostly small boulders on a layer of cobble set in gravel. Sea urchins (*Strongylocentrotus*

droebachiensis) were abundant in both areas and especially dense in a grazing front located about midway between the areas. A fish meal plant 1 km to the north operated intermittently and may have provided some organic input.

The sites were chosen because crabs and lobsters were abundant, habitats with and without macroalgal cover were close together, kelp cover was not too dense for divers to census crabs and lobsters, and depth (<10 m) and underwater visibility (5–10 m) were not restrictive to divers. Also, most rocks that might shelter a crab or lobster could be overturned by a diver, and protection from ocean swells permitted work in most weather conditions.

Diver Survey

Divers surveyed 15, 40-m^2 transects, for a total of 600 m^2 in each habitat. A weighted line, 120 m long and numbered at 5-m intervals, was placed along the deep edge of each habitat. Starting at a 5-m mark chosen from a random numbers table, a diver laid out a disposable 40-m string by proceeding up slope on a compass course. After returning to the start of the transect, one diver carefully searched for lobsters and crabs in a 1-m wide band the length of the string while the other diver watched for lobsters or crabs which might escape from the path of the first diver. The width of the band was measured by a rod moved along the string. Lobsters ≥40 mm carapace length (CL) and crabs ≥60 mm carapace width (CW) were captured, measured underwater in 10-mm intervals with calipers, and released where captured. A few of the lobsters that were flushed from under rocks escaped capture, and their sizes were estimated. Sizes were recorded by the divers. The physical qualities of the study area, practice transects run by the divers, and careful searching during the survey gave us confidence that few lobsters or crabs of the desired sizes were overlooked.

Diver counts were made between September 8 and 21, 1983. Lobsters are most visible and most easily trapped soon after molting (pers. obs.). In this area most molting occurs in August.

Confidence intervals on the mean number of crabs per square metre in discrete size groups were calculated after data transformation by $\log_e((Y+0.5)/120))$. Y is the sum of counts for three adjacent 40-m^2 transects, 0.5 is added to eliminate remaining zeros, and the sum is divided by 120 to convert the count to crabs per square metre. After taking the $\log_e$ of these values, frequency distributions were more nearly normal and variances were independent of the means. Confidence intervals (CI) were calculated from these values in the usual manner. The antilog of the CI is given, and can be multiplied and divided by the arithmetic mean to obtain 95% CI on the mean number per square metre. Since the arithmetic mean was not transformed it did not need to be untransformed (Cassie 1968). Meaningful confidence intervals could not be calculated for numbers of lobsters within size groups because of the high frequency of zero counts on transects.

Lobster CL (in millimetres) and crab CW (in millimetres) were converted to live weight (W in grams) with the equations $W=0.00168\ CL^{2.828}$ (Thomas 1973) and $W=0.0001136\ CW^{3.060}$ (Scarratt and Lowe 1972), respectively. Biomass (x) for each species on each transect in each habitat was transformed by $\log_e(x+1\ g)$ before calculating CI as above, and testing for biomass differences between habitats.

Trapping Surveys

Traps were 68 by 58 by 36 cm high made mostly of wood, and of a type used in the local lobster fishery (as in figure 1 of Krouse and Thomas (1975), but without an escape vent). Two opposite side entrances led to a compartment where the bait was located, and an internal entrance led to a second compartment. Traps were baited daily with 0.5 kg of frozen mackerel (*Scomber scombrus*). Lath spacings of 2 cm on the sides of traps determined the minimum crab size retained at about 60 mm CW (the maximum size that could be passed between the laths by hand), and the minimum lobster size retained at 40–50 mm CL (Krouse and Thomas 1975).

Traps were set for 20–26 h on three successive days in September 1983. Bottom temperature was 13°C. Ten traps were spaced about 20 m apart within each habitat and located by referring to six surface buoys outlining each habitat. Crabs ≥60 mm CW and lobsters ≥40 mm CL were measured in 10-mm intervals and returned to the water within 10 m of where they were caught. Even though traps were fished on successive days in a small area, there was no evidence that attraction of the bait caused accumulation of lobsters or crabs. A two-way ANOVA for each species compared catches among days (after $\log_e$ transformation) and showed no difference in mean catch per trap (below) ($F=0.6$, $P>0.1$ for lobsters; $F=0.1$, $P>0.1$ for crabs) or no day × habitat interaction ($F=0.5$, $P>0.1$ for lobsters; $F=0.3$, $P>0.1$ for crabs).

	Lobster catch per trap			Crab catch per trap		
	Date			Date		
Habitat	27/IX	28/IX	29/IX	27/IX	28/IX	29/IX
Kelp	4.0	4.6	4.2	18.8	18.4	19.5
Barrens	4.1	4.0	3.4	9.8	12.2	14.1

The weights of catch per trap were obtained with the weight–length regressions and $\log_e$ transformed before calculating confidence intervals or comparing means between habitats.

Results

Assuming that diver counts represented the actual size frequency of lobsters and crabs, then traps were highly selective for larger animals. Traps operated selectively for both species in both habitats (Fig. 1). For example, for both habitats combined, 41% of trap catches but only 4% of diver counts were lobsters ≥80 mm CL. Also, 30% of catches, but only 13% of counts, were crabs ≥90 mm CW.

Catchability coefficients ($(c/f)/D$) also demonstrated the higher catchability of larger animals (Table 1). Lobsters 50–59 mm CL were one-fourth as catchable as those 60–69 mm CL in both habitats, i.e. 13 versus 47 and 14 versus 51 $m^2 \cdot trap^{-1}$ for kelp and barrens, respectively. Both sizes had very low catchabilities compared with lobsters 70–89 mm CL, 492 and 255 $m^2 \cdot trap^{-1}$ for kelp and barrens, respectively. Catchabilities for lobsters ≥90 mm CL would have been even larger, but q was not calculated because only one lobster of this size was encountered in the 1200 m^2 surveyed by divers. Crabs 60–79 mm CW had catchabilities only 15 and 33% as high as the catchabilities in the ≥80 mm size group.

The study areas should have been bigger to measure q for the larger crabs and lobsters. One-eighth of each study area (600 m^2) was censused by divers. Only three lobsters ≥80 mm CL were counted in both areas combined, giving an estimated population of 24 lobsters. Yet, the largest catch in the 3 d of trapping was 41 lobsters of this size. Twenty-one crabs ≥90 mm CW were counted in both areas, indicating a population of

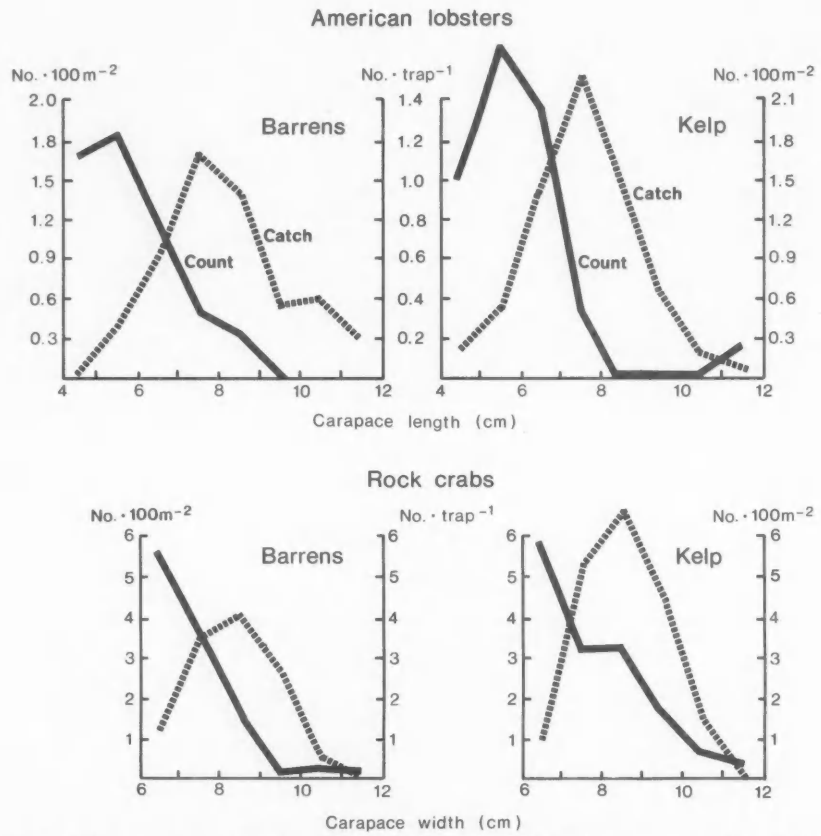

FIG. 1. Size frequencies of American lobsters and rock crabs obtained by diver count and trap catches from both barren (without macroalgae) and kelp (abundant macroalgae) habitats.

168. The largest day's catch of these large crabs was 99, an improbably high fraction of the population. Crab and lobster densities on the periphery of the study areas were not measured, but divers estimated that they were similar to or lower than that found within the study areas. These outlying areas no doubt supplied some of the large crabs and lobsters to trap catches.

The catchabilities for a given crab or lobster size group differed by less than a factor of two between kelp and barren habitats, and is probably not significantly different for any comparison (Table 1). No statistical tests were used because only one q was available for each species–size–habit combination. The largest difference in catchability between habitats was for lobsters 70–89 mm CL. Divers counted only three and five of these individuals in kelp and barrens, respectively.

If size frequencies from diver counts differed between habitats, size frequencies from trap catches differed also (Table 2). Both divers and traps sampled more big crabs in kelp than in barrens ($P<0.05$). Size frequencies of lobsters <100 mm CL were similar in kelp and barrens for both diver and trap samples ($P>0.1$). Lobsters ≥100 mm CL were more abundant from trap catches in barrens ($P<0.1$), but these sizes were too rare to appear in diver counts.

The relative biomass in the two habitats was also reflected in both diver and trap samples (Table 3). Mean lobster biomass in kelp and barrens was not different ($P>0.1$) when sampled by either method. Both diver and trap sampling of crabs gave a higher biomass in kelp ($P<0.05$).

Discussion

Habitat

Catchability coefficients obtained on shallow bottoms with high relief have been in the tens of hundreds of square metres per trap, whereas values from deep, flat bottoms have been in the thousands of square metres. However, independent of identifiable causes, catchabilities have high variability within and among target species (Table 4). Two studies were conducted on western Australian rock lobster inhabiting shallow limestone reefs. Chittleborough (1970) used a trap–mark–recapture method to measure lobster density, and catchabilities were reported in January for five successive years at one to three locations each year. Moon phase, soak time, temperature, and molt stage were near constant for all measurements. Estimates of q among locations within a year were in close agreement, e.g. 144, 164, and 174 $m^2 \cdot trap^{-1}$, however, among years the range was 25–174 $m^2 \cdot trap^{-1}$ (CV = 57%, $N = 9$). On a single reef further north, Morgan (1974) also measured lobster density using a trap–mark–recapture method and estimated q for 34 of 38 successive months. After standardizing for soak time and moon phase in the sampling design, and using a multiple

TABLE 1. Catchability coefficients (q, in square metres per trap) for American lobsters and rock crabs in kelp and barren habitats. Animal size: CL in millimetres for lobsters and CW in millimetres for crabs.

Habitat	Animal size (CL/CW)	No. trap hauls	Total catch	No. animals per trap	Factor[a]	Total count	No. animals per square metre	Factor[a]	q
				Lobsters					
Kelp	50–59[c]	28	9	0.32	[b]	15	0.025	[b]	13
	60–69	28	26	0.93	[b]	12	0.020	[b]	47
	70–89	28	69	2.46	1.14	3	0.005	[b]	492
	≥90	28	17	0.62	[b]	1	~0	[b]	[d]
Barrens	50–59[c]	28	7	0.25	[b]	11	0.018	[b]	14
	60–69	28	17	0.61	[b]	7	0.012	[b]	51
	70–89	28	57	2.04	1.35	5	0.008	[b]	255
	≥90	28	26	0.93	[b]	0	0	[b]	[d]
				Crabs					
Kelp	60–79	28	175	6.3	1.52	54	0.090	1.79	70
	≥80	28	357	12.8	1.19	36	0.060	1.99	213
Barrens	60–79	28	133	4.8	1.48	57	0.095	1.52	51
	≥80	28	209	7.5	1.32	13	0.022	1.70	339

[a]95% Confidence interval is obtained by multiplying and dividing the number of animals per trap or number of animals per square metres by this factor.
[b]Lobster counts or catches were too low to calculate confidence interval.
[c]Lobsters 40–49 mm CL excluded because of possible escapement from traps.
[d]Census area of 600 m^2 too small to calculate q for larger lobsters.

TABLE 2. Chi-square analyses comparing size frequencies between kelp and barren habitats for each of rock crab counts, rock crab catches, American lobster counts, and American lobster catches.

	Crab counts Mean size (mm CW)					**Lobster counts** Mean size (mm CL)				
	65	75	85	>90	Σ	45	55	65	>70	Σ
Kelp	35	19	19	17	90	9	15	12	4	40
Barrens	34	23	9	4	70	10	11	7	5	33
	$\chi^2 = 9.6$ ($0.05 > P > 0.01$)					$\chi^2 = 1.6$ ($P \gg 0.10$)				

	Crab catches Mean size (mm CW)						**Lobster catches** Mean size (mm CL)						
	65	75	85	95	>100	Σ	55	65	75	85	90	>100	Σ
Kelp	28	147	186	126	45	532	9	26	42	27	12	5	121
Barrens	35	98	116	75	18	342	7	17	31	26	10	16	107
	$\chi^2 = 10.6$ ($0.05 > P > 0.01$)						$\chi^2 = 10.0$ ($0.1 > P > 0.05$); $\chi^2 = 0.5$ ($P \gg 0.1$) if lobsters >100 mm CL omitted						

TABLE 3. Mean biomass of American lobsters and rock crabs in kelp and barren habitats: estimates from diver counts, grams per square metre, and trap catches, kilograms per trap.

	Species/size	Kelp	Factor[a]	Barrens	Factor[a]	t	P
Counts	Lobsters ≥40 mm	12.8	1.8	9.8	1.7	1.4	>0.10
	Crabs ≥60 mm	11.6	1.4	7.2	1.4	2.2	<0.05
Catches	Lobsters ≥40 mm	1.8	1.3	1.8	1.2	0.2	>0.10
	Crabs ≥60 mm	1.9	1.2	1.1	1.4	3.6	<0.01

[a]95% Confidence intervals can be obtained by multiplying and dividing the mean biomass by this factor.

TABLE 4. Review of catchability coefficients (q) in square metres per trap.

Species	Size	q	Reference
Panulirus cygnus	>30 mm CL	25–174	Chittleborough (1970)
	>50 mm CL	33–120	Morgan (1974)
Chionoecetes opilio	>90 mm CW	2500–5300	Miller (1975)
Geryon maritae	> 60 mm CW	2160	Melville-Smith (1986)
Five taxa of tropical reef fish	>100 mm or >200 mm fork length	140–350	Miller and Hunte (1987)
Homarus americanus	>50 mm CL	13–492	this study
Cancer irroratus	>60 mm CW	51–339	this study

regression equation to standardize for temperature, salinity, and stage of molt cycle, q was 33–120 $m^2 \cdot trap^{-1}$ (CV = 38%, $N = 34$).

Densities of deep-water (200 and 500 m) crabs have been measured using bottom photography. The *Chionoecetes* study was mostly on flat mud bottom. The *Geryon* habitat was not described, but because of the uniform depth presumably it was similar. Catchability of *Chionoecetes* ranged from 2500–5300 $m^2 \cdot trap^{-1}$ over four locations (CV = 29%) (Miller 1975), and the single value for *Geryon* was 2160 $m^2 \cdot trap^{-1}$ (Melville-Smith 1986).

Miller and Hunte (1987) censused five taxa of reef fishes by diving on two shallow reefs in Barbados, West Indies. Catchabilities (for unbaited traps) on two reefs were 141 and 148 $m^2 \cdot trap^{-1}$ for parrotfish, and 134 and 194 $m^2 \cdot trap^{-1}$ for surgeonfish. Catchabilities for squirrelfish, angelfish, and a grouper measured on one reef each were 348, 346, and 335 $m^2 \cdot trap^{-1}$.

In the Louisbourg study a given crab or lobster size had similar catchabilities in both kelp and barrens. Although traps were selective for large animals, catches nevertheless reflected the habitat differences in size frequencies seen in diver counts. Also, data from catches and counts agreed on the relative biomass in the two habitats. The presence of lobsters in traps may have deterred some crabs from entering, as shown experimentally by Richards et al. (1983). However, numbers of lobsters and crabs per trap were not correlated for either kelp ($r = -0.04$) or barrens ($r = -0.10$) habitat.

Only a small number of measurements of q are available for any trap type, environmental condition, or target species. Because of the effort required to measure q, the number of estimates compared with the number of important variables will remain few for the foreseeable future. In fact, q's adequate to assess abundance of any target species are probably not available. These observations suggest that investigators should hold constant as many variables as practical, e.g. target species, season, trap type, soak time, and bait, and concentrate on measuring q for the variables that are not practical to standardize, e.g. animal size and habitat.

Animal Size

Small decapods have often been shown to be underrepresented in trap catches. A faster walking rate (McLeese and Wilder 1958), more hours of activity per day (Chapman and Howard 1979; Lawton 1987), winning agonistic encounters near traps (Scrivener 1971), and a smaller chance of escape through the entrance (R. Semple, Department of Fisheries and Oceans; D. Maynard, Department of Fisheries and Oceans; and H. Price, Dalhousie University, have observed that small American lobsters are more likely to escape than large, pers. comm.) may all contribute to the higher catchability of larger animals. Small animals can also escape through spaces in the material covering a trap, but in this study and in those reviewed below, selectivity is considered for only those sizes that could not escape in this way.

Smith (1944) tagged trap-caught American lobster before the fishing season at five locations in the southern Gulf of St. Lawrence, then recorded the sizes recaptured by the fishery. At all locations the percentage recaptured increased with size; from 60 to 80 mm CL the average percentage recaptured increased by a factor of 1.7. Ennis (1978 and pers. comm.) obtained size frequencies of American lobster in Newfoundland by diving and trapping in the same area at about the same time. Assuming that the diver samples were an unbiased index of abundance, the larger males (81–105 mm CL) were 12 times more vulnerable to trapping than smaller males (61–80 mm CL) and the larger females were six times more vulnerable than smaller females. Morrissy and Caputi (1981) trapped freshwater crayfish in small ponds, drained the ponds, then measured size distributions of the populations. Over about a three-fold increase in CL, the probability of capture increased from three to sevenfold when measured at three temperatures. Carroll (1982 and pers. comm.) trapped, tagged, released, and retrapped *Cancer antennarius* in California. Recapture rates for crabs 125–144 mm CW were four times higher than for those 80–94 mm CW.

The chance of recapture also increased with size for a large portunid crab in Queensland, Australia (Williams and Hill 1982). For crabs trapped, tagged, and released, recapture rates were 3.3 times higher for males and 4.5 times higher for females of 150 mm CW compared with 100 mm CW. The authors noted that capturing and recapturing by the same method, included only crabs vulnerable to trapping. If the initial capture had been by a different method the difference in recapture rates with size might have been even larger. The same comment would apply to Smith's (1944) and Carroll's (1982) studies mentioned above. Although the above studies estimate relative catchability of different sized decapods, catchability in units of area cannot be calculated because animal density was not measured.

Average catchability in the two habitats in Louisbourg increased by more than an order of magnitude from lobster sizes of 50–59 to 70–89 mm CL, and by a factor of three or seven (depending on habitat) from crab sizes of 60–79 to ≥80 mm CW.

Given this size selectivity, a large bias in calculated fishing mortality (F) would result from an assumption that different ages are equally vulnerable to trapping. For example, if catch per trap averaged three lobsters of age t and two of age $t+1$, then from

$$c/f_t = c/f_{t+1}\, e^{F+M}$$

F + M would equal 0.4. If annual natural mortality (M) was 0.1 for both ages, then annual fishing mortality would equal 0.3.

However, if age $t+1$ was twice as vulnerable to trapping as age t, then the true relative densities would be 1:3 rather than 2:3, F+M would be 1.1 and F would be 1.0 rather than 0.3.

Four studies on spiny lobster have shown inconsistent effects of size on trapability. Morgan (1974) found similar size frequencies for trap-caught and diver-caught *Panulirus longipes* of both sexes. However, by trapping in a large tank he showed that males 76–85 mm CL were twice as likely to be captured, and females of the same size three times as likely to be captured, as those >85 mm CL (Morgan 1979). Male *Jasus lalandii* >100 mm CL were present in diver samples from each of five stations in South Africa, but virtually absent in trap catches (Newman and Pollock 1974). However, in a later diving–trapping study on both sexes of the same species, Pollock and De B. Beyers (1979) found lobsters >80 mm CL about 10% more trapable than those 70–80 mm CL.

In conclusion, trap catches greatly underestimated abundance of small relative to large crabs and lobsters on the fishing ground. Because large animals were in low density, future studies of this type need to include a larger area of bottom. Trap catches reflected diver measured similarities or differences in size frequency or biomass between kelp and barren habitats. Also, the similar size of catchability coefficients for kelp and barren habitats give encouragement that robust size specific catchability coefficients might be determined for these species.

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Factors Affecting Alkalinity Concentrations of Streamwater during Snowmelt in Central Ontario

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Relative contributions of changes in base cations and acid anions to alkalinity decreases during spring snowmelt in 1984–86 were analyzed for 15 headwater streams and lake outflows in three central Ontario catchments. During episodes, concentration changes in ions which contributed to alkalinity decreases were partially offset by smaller changes in other ions which contributed to alkalinity increases. The major contributor to alkalinity depressions was base cation dilution by snowmelt water. Akalinity depressions were more likely to be dominated by SO_4^{2-} increases in streams that were more acidic. Neither nitrate nor organic acid anions were significant contributors to alkalinity depressions. Discharge was highly correlated with alkalinity in a circumneutral stream but not in an acidic stream and is consistent with dilution being less important as a cause of alkalinity depressions as streams become more acidic.

On a étudié l'influence relative qu'exercent sur la baisse de l'alcalinité les changements touchant les cations des bases et les anions des acides durant la fonte des neiges aux printemps de 1984 à 1986 dans les eaux de 15 cours d'eau de tête et émissaires de lacs, dans trois bassins versants du centre de l'Ontario. Durant les épisodes, les changements de concentration d'ions qui ont concouru aux baisses d'alcalinité étaient en partie contrebalancés par des changements moins marqués de la concentration d'autres ions qui concouraient à l'augmentation de l'alcalinité. La dilution des cations des bases par l'eau de fonte est le principal facteur de la baisse d'alcalinité. Dans les cours d'eau plus acides, il était plus probable que les baisses d'alcalinité soient déterminées principalement par une augmentation de SO_4^{2-}. Ni les anions des nitrates, ni ceux des acides n'ont concouru dans une mesure significative aux baisses d'alcalinité. On a constaté une forte corrélation entre le débit et l'alcalinité dans un cours d'eau où le pH est proche du point neutre, mais non dans un cours d'eau acide, ce qui confirmerait que la dilution est un facteur de baisse d'alcalinité moins important dans les cours d'eau qui s'acidifient.

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Depressions of pH and alkalinity in streams and lakes as a consequence of snowmelt are well documented over both a broad geographical scale and over a wide range of alkalinity (Gjessing et al. 1976; Henriksen and Wright 1977; Hultberg 1977; Jeffries et al. 1979; Galloway et al. 1980, 1987; Bjarnborg 1983; Keller 1983; Sharpe et al. 1984; Gunn and Keller 1984, 1986; Jacks et al. 1986; Baird et al. 1987; Stoddard 1987). These episodic depressions are caused by base cation dilution (Galloway et al. 1980, 1987; Jacks et al. 1986; Stoddard 1987) and/or acid anion increases (Galloway et al. 1980, 1987; Galloway and Dillon 1983; LaZerte and Dillon 1984). This follows from the secondary (or charge balance) definition of alkalinity (Schindler et al. 1986):

$$(1)\quad \mathrm{Alk} = \mathrm{Ca^{2+}} + \mathrm{Mg^{2+}} + \mathrm{Na^{+}} + \mathrm{K^{+}} + \mathrm{NH_4^{+}} + \Sigma\mathrm{Al^{+}} - \mathrm{SO_4^{2-}} - \mathrm{NO_3^{-}} - \mathrm{A^{-}} - \mathrm{Cl^{-}},$$

where Alk is bicarbonate alkalinity ($-\mathrm{HCO_3^-} + \mathrm{CO_3^{2-}} + \mathrm{OH^-} - \mathrm{H^+}$) and where $\mathrm{A^-}$ represents the charge contributed by dissociated strong and weak organic acids and $\Sigma\mathrm{Al^+}$ represents the sum of the charged inorganic aluminum species; all parameters are expressed in microequivalents per litre.

The contribution of base cations to alkalinity may be overestimated when organic acid-cation complexation occurs because most analytical measurements of base cations yield total values, while the proportion of complexed cations cannot be determined.

There is some concern that anions such as SO_4^{2-} and NO_3^- may dominate alkalinity depressions in areas of high acid deposition because anions accumulated during the winter in the snowpack are released during a relatively brief melt period (Johannessen et al. 1977; Cadle et al. 1984; English et al. 1986; Stottlemyer 1987; Wyer and Hill 1984; Warwick and Hill 1988) when biological activity in soil and stream sediments is low because of low temperatures. Biologically-mediated reduction of these anions consumes acidity (Brewer and Goldman 1976; Schindler et al. 1985).

The quantitative contribution of anions and cations to alkalinity depressions is complicated by early release of ions from snowpack before maximum discharge is reached (Johannessen

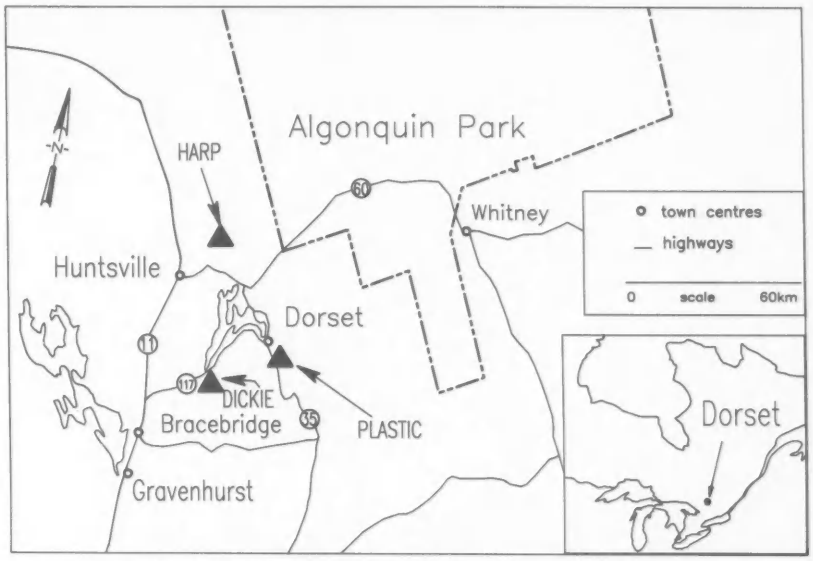

FIG. 1. Map of central Ontario showing locations of study sites.

et al. 1977; Jacks et al. 1986; Christophersen et al. 1984). Anion concentrations in streams may peak well before minimum alkalinities are observed (Jacks et al. 1986), indicating that base cation dilution is at least partially responsible for alkalinity reduction.

This paper presents an analysis of the causes of short-term (episodic) acidification in streams. The relative contributions of major ions to alkalinity depressions during spring melt in 3 yr (1984–86) are presented for 15 headwater streams and lake outflows in three central Ontario watersheds.

Materials and Methods

Study Areas

Harp and Dickie Lakes are located in the District of Muskoka, and Plastic Lake is located in Haliburton County, central Ontario (Fig. 1). Plastic Lake is the most acidic (whole-lake alkalinity approximately 15 $\mu eq \cdot L^{-1}$ in 1980, 5 $\mu eq \cdot L^{-1}$ in 1985) with measurable decreases in pH and alkalinity occurring since 1979 (Dillon et al. 1987). Harp Lake is the least acidic but is still considered acid-sensitive with whole-lake alkalinity 61 $\mu eq \cdot L^{-1}$ and pH 6.3 in 1985. Catchment characteristics are listed in Table 1.

The lakes are underlain by Precambrian metamorphic silicate bedrock. The Plastic Lake catchment has surficial deposits of thin Pleistocene glacial till (<1 m) on bedrock and peat overlying layers of clay and sand. The Harp Lake catchment is partially covered by a till plain (>1 m), with the remainder being thin till with exposed rock ridges. Smaller deposits of sand and peat (overlying sand) occur. The Dickie Lake catchment consists primarily of thin till and exposed rock ridges with smaller deposits of till and peat overlying clay or sand. More detailed descriptions of the geology and physiography of the catchments can be found in Jeffries and Snyder (1983); LaZerte and Dillon (1984); Girard et al. (1985); Seip et al. (1985); and Dillon et al. (1987).

The watersheds are primarily forested with some cottage development around Harp and Dickie Lakes.

TABLE 1. Catchment characteristics of study sites

Lake		Area (ha)	Bedrock geology[a]	Surficial geology[b]
Harp	Inflow 3	26.0	1	10
	Inflow 3A	19.7	1,3	10
	Inflow 4	119.6	3	10,7,8
	Inflow 5	190.5	1	10,7,6,8
	Inflow 6	10.0	2,1	7,10
	Inflow 6A	15.3	1	7
	Outflow 0	542.5[c]	—	—
Plastic	Inflow 1	23.3	4	7
	Outflow 0	127.6[c]	—	—
Dickie	Inflow 5	30.0	5	7,9
	Inflow 6	21.8	5	7,9
	Inflow 8	67.0	5	7,10,9
	Inflow 10	78.9	5	7,9
	Inflow 11	76.3	5	7,9
	Outflow 0	500.4[c]	—	—

[a]1 = Granitized biotite and horneblende gneiss, 2 = diorite, 3 = amphibolite and schist, 4 = ortho-gneiss, 5 = horneblende migmatite.

[b]6 = Peat over sand, 7 = thin till and rock ridges, 8 = sand, 9 = peat over clay over sand, 10 = minor till plain.

[c]Includes lake area plus ungauged inflowing tributaries.

Sample site codes are denoted by HP (Harp), DE (Dickie), and PC (Plastic). Inlet streams are numbered from 1–11 and lake outlets are coded as 0, i.e. the outlet from Harp Lake is coded as HP0.

Sample Collection and Analytical Techniques

Water collection (Locke and Scott 1986), analytical techniques (OME 1983), and hydrologic methods (Scheider et al. 1983) are described in detail elsewhere. Briefly, weirs or flumes were installed at the mouth of 12 inlet streams and at three lake outlets. Samples were collected as frequently as possible (>1 wk; average of four times per week) during spring melt in 1984,

TABLE 2. Maximum alkalinity decrease (microequivalents per litre) relative to preepisode value, episode duration, and number of days sampled (n) for each alkalinity depression in Harp, Plastic, and Dickie streams. The No. 1 and No. 2 refer to cases where there were multiple episodes in a single year.

Site	ΔAlk_{max}	Days	n
1984 No.			
HPO 1	17	32	22
HPO 2	17	21	11
HP3	48	29	21
HP3A	24	24	19
HP4	15	30	22
HP5	47	28	21
HP6 No. 1	24	22	17
HP6 No. 2	31	41	22
PC0	10	59	38
PC1	22	34	20
DE0	17	48	28
DE5 No. 1	51	33	21
DE5 No. 2	41	41	27
DE6	27	49	27
DE10	6	35	23
DE11	27	33	19
1985			
HP0	27	39	17
HP3	60	68	67
HP4	88	81	74
HP5	59	80	71
HP6	40	81	70
PC0	21	28	9
PC1 No. 1	31	28	16
PC1 No. 2	17	44	21
DE0	23	61	24
DE6	32	36	37
1986			
HP3	80	59	37
HP4	111	63	40
HP5	97	63	39
HP6	69	69	39
HP6A	24	46	29
PC1 No. 1	16	28	9
PC1 No. 2	77	59	21
DE5	67	42	18
DE6 No. 1	18	21	10
DE6 No. 2	20	21	7
DE8	21	39	18
DE10	18	47	21

1985, and 1986, filtered through 76-μm Nitex mesh into appropriate prerinsed sample bottles, and placed in temperature-controlled containers to prevent freezing. Samples were routinely analyzed for alkalinity by modified Gran titration, pH, NH_4^+, Cl^-, SO_4^{2-}, NO_3^+, Ca^{2+}, Mg^{2+}, Na^+, K^+, and dissolved organic carbon (DOC). Organic acid anion concentration (A^-) was estimated as a function of DOC and pH (Oliver et al. 1983; LaZerte and Dillon 1984).

Data Analysis

There are three methods of estimating alkalinity. Bicarbonate alkalinity can be calculated from equation (1) using measurements of all parameters on the right-hand side of the equation. This is the least desirable method since the error in the result includes the errors in all of the terms of the right-hand side. Bicarbonate alkalinity can also be estimated from dissolved inorganic carbon (DIC) and pH measurements using theoretical speciation relationshps for the inorganic carbon species; too few DIC measurements were made to utilize this method effectively. Finally, alkalinity can be measured directly by titration; the Gran method employed in our study includes not only the bicarbonate alkalinity but some alkalinity attributable to other sources including titration of organic acids and possibly some aluminum species. Nevertheless, we have chosen to use the latter for two reasons. The difference between the Gran alkalinity and the bicarbonate alkalinity is generally small, typically being between 5 and 25% (P. Dillon and B. LaZerte, unpubl. data) with the greater differences usually (but not always) found in waters with high DOC content. These differences should be lowest during snowmelt because the snow itself has very low DOC concentration. The aluminum levels observed in these streams were generally low compared with the levels of other components of the measured Gran alkalinity. For example, LaZerte (1984) showed that the change in total inorganic monomeric aluminum in PCl, during the snowmelt period of 1982 reached a maximum of ~5 $\mu eq \cdot L^{-1}$ (assuming an average charge of $^{2+}$ on the aluminum species); the aluminum levels in our other study streams were lower. Since only a part (if any) of this aluminum is likely to be included in the titration, this is an upper estimate of the error contributed by this factor when the Gran titration alkalinity is assumed to approximate the bicarbonate alkalinity. The second reason that we used Gran alkalinity is that it is frequently measured and used as the standard indicator of lake/stream acid neutralizing capacity.

Alkalinity decreases were delineated by visual inspection of alkalinity versus time plots. Only large, visually obvious decreases lasting a minimum of 3 wk were included (Table 2). A total of 38 episodes were defined by inspection of 43 stream-years of data. Subsequently, daily changes in alkalinity, SO_4^{2-}, NO_3^-, A^-, and C_b ($Ca^{2+} + Mg^{2-} + Na^+ + K^+$) were calculated as the difference between the daily value during an episode and a preepisode value. Ammonium, Cl^-, and ΣAl^+ were ignored because their contributions were minor. The preepisode value that we used was usually the discrete value immediately prior to the episode. However, in 1984, preepisode values were relatively constant for approximately 4–6 wk prior to the depressions, and mean preepisode values were used for DEO, DE10, PCO, PCl, HP4, HP5, and the first of multiple episodes for HP0, HP3A, and HP6. Daily ion-specific contributions to alkalinity increases and decreases during alkalinity depressions (df_i) were then calculated as $\Delta SO_4^{2-}/\Delta alk$, $\Delta NO_3^-/\Delta alk$, $\Delta C_b/\Delta alk$, and $\Delta A^-/\Delta alk$ where:

(2) $\Delta alk = \text{alkalinity (day 0)} - \text{alkalinity (day } i\text{)}$

(3) $\Delta C_b = C_b \text{ (day 0)} - C_b \text{ (day } i\text{)}$

(4) $\Delta SO_4^{2-} = SO_4^{2-} \text{ (day } i\text{)} - SO_4^{2-} \text{ (day 0)}$

(5) $\Delta NO_3^- = NO_3^- \text{ (day } i\text{)} - NO_3^- \text{ (day 0)}$

(6) $\Delta A^- = A^- \text{ (day } i\text{)} - A^- \text{ (day 0)}.$

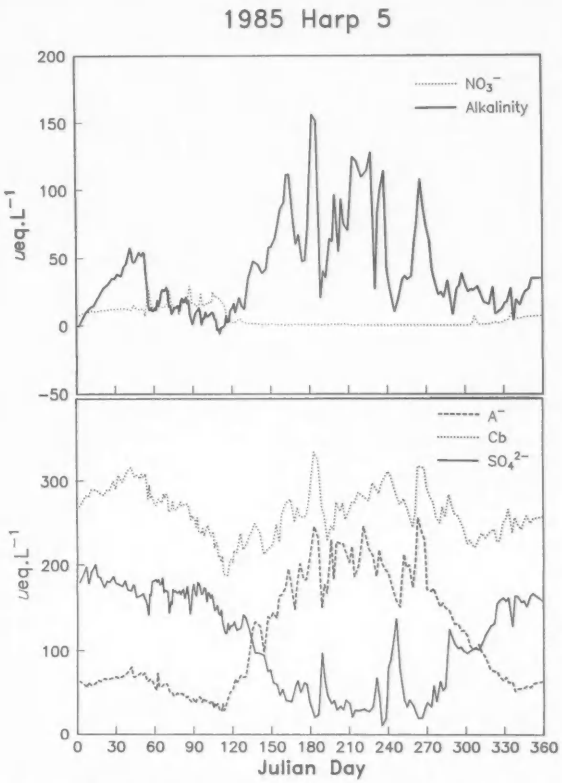

FIG. 2. Daily alkalinity, NO_3^-, C_b, SO_4^{2-}, and A^- in Harp 5 in 1985.

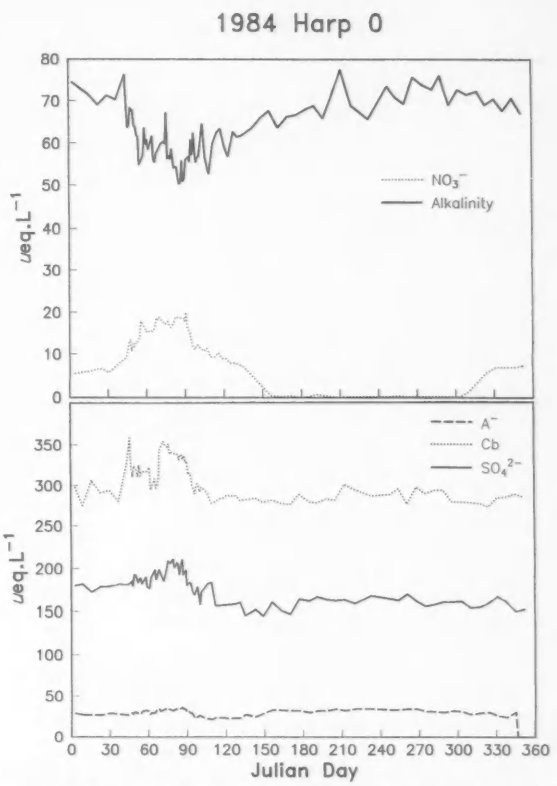

FIG. 3. Daily alkalinity, NO_3^-, C_b, SO_4^{2-} and A^- in Harp 0 in 1984.

The magnitude of the alkalinity change, Δalk, is the result of the net change in ion concentrations. Positive values of df_i denote contributions to alkalinity decreases and negative values denote contributions to alkalinity increases. Positive and negative values may occur simultaneously, for example when both anions and cations are diluted.

The theoretical sum of the four contributions on any given day (Σdf_i) is *1*, ignoring minor ions and contributions of minor factors including organic acids and aluminum species to the Gran titration. These considerations do not affect the relative importance of the major contributors to alkalinity decreases, but only the fact that the sum of the effects should approach 1.0.

Results and Discussion

Seasonal cycles of C_b, SO_4^{2-}, and NO_3^- concentrations were discernible during the year in the Harp, Plastic, and Dickie inflows. Minimum C_b typically occurred during spring melt (days 90–150) while minimum SO_4^{2-} (<100 μeq·L^{-1}) occurred during summer months (days 150–200) (Fig. 2). C_b and SO_4^{2-} concentrations typically ranged from 100–500 μeq·L^{-1} during the year.

Nitrate concentrations were much less than C_b and SO_4^{2-} with high values observed during spring melt and low values near the detection limit observed during summer months (Fig. 2). A maximum of 110 μeq·L^{-1} was observed in HP5 on February 15, 1984. Increases were typically observed during spring melt and were of short duration in inflows.

Lake outflow chemistry differed from inflow chemistry. The extent of seasonal fluctuations in C_b and SO_4^{2-} were less and NO_3^- increases lasted longer in outflows (Fig. 3).

Thirty-eight spring melt episodes from 12 inlets and three outlets were analyzed for the period of 1984–86. In a few sites in some years there were no marked alkalinity decreases during snowmelt. During most episodes, concentration changes in ions which contributed to alkalinity decreases were typically offset by smaller changes in other ions which contributed to alkalinity increases (Fig. 4). For example, in HP5 in 1985 C_b dilution was accompanied by anion dilution (Figs. 2 and 4). Occasionally, two episodes were observed in a stream during spring melt. Maximum alkalinity decrease, episode duration and number of sampling days per episode are listed in Table 2.

The average Σdf_i values for all streams and years for Plastic and Harp Lake inflows and outflows (Table 3) ranged from 0.68 to 0.81. Although the value for Dickie Lake was −0.10, the result was not significantly different from 1.0. High values of $\Sigma A^-/\Sigma Alk$ in Dickie Lake appear to have caused the low Σdf_i suggesting that A^- may have been overestimated or that the difference between Gran alkalinity and bicarbonate alkalinity was greatest here. Organic acid anions did not contribute to alkalinity depressions in Dickie Lake inflows despite high con-

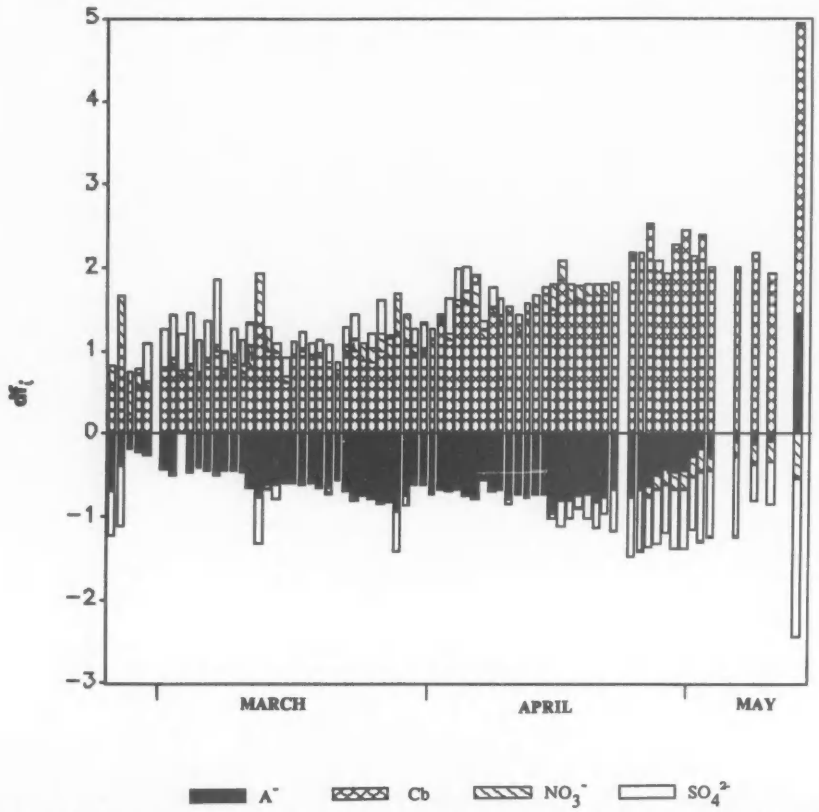

FIG. 4. Relative daily contributions of changes in C_b, SO_4^{2-}, NO_3^-, and A^- to alkalinity depressions (df_i) in HP5 in 1985. Contributions are expressed as Δion/Δalk where Δ is the difference between a preepisode value and the concentration on a given day. Positive values denote contributions to an alkalinity depression whereas negative values represent alkalinity increases.

centrations; depressions in these streams were characterized by dilution of A^-.

The major contributor to alkalinity depressions was C_b dilution (i.e. the largest positive df_i numbers in Table 3) although the contribution of C_b dilution in Dickie streams may have been overestimated because significant DOC–cation complexation may have occurred.

In general, during the melt periods of 1984 to 1986, NO_3^- increases contributed to alkalinity depressions to a much smaller extent than C_b dilution (Table 3). The larger of the NO_3^- contributions occurred in HPO (first episode), HP3A, HP5, PCO, and DEO in 1984 and HPO in 1985 (Table 3). The only alkalinity depression dominated by NO_3^- increases occurred in DEO in 1984 but only in the first 2 wk of the 7-wk depression. Nitrate typically contributed to depressions early in episodes in inflow streams but was more evenly distributed over time during depressions in lake outflows.

Alkalinity depressions dominated by SO_4^{2-} contributions were observed in HPO (first episode), PCO, DEO, and DE5 (both episodes) in 1984, PC1 (fist episode), and DE6 in 1985, and HP6A, PC1 (both episodes), DE5, DE6 (both episodes), and DE10 in 1986. These SO_4^{2-} contributions were accompanied by either C_b dilution or increases.

Depressions were more likely to be dominated by anion increases as the degree of acidification increased whereas cation dilution was more likely to dominate depressions in circumneutral systems. Sulphate-dominated depressions occurred proportionately more often in the more acidic Plastic and Dickie catchments than in the Harp catchment (86% of the 14 SO_4^{2-}-dominated depressions occurred in Plastic and Dickie streams although only 53% of the episodes were in these two catchments). In the outflows of three Adirondack lakes covering a range of acidic conditions (pH 5–7), during spring melt in 1978–80 cation dilution was much larger than the anion increase in more alkaline Panther Lake (pH 7) whereas in acidic Woods Lake (pH 5), C_b dilution was much smaller (Galloway et al. 1980, 1987). The dominant anion was primarily NO_3^-, unlike central Ontario. Higher NO_3^- concentrations in Adirondack streams may result from differences in surficial catchment geology, forest types or higher areal water discharge rates (Dillon and Molot, unpubl. data) because atmospheric deposition rates are similar in the two regions (30–40 $meq \cdot m^{-2} \cdot yr^{-1}$). Intermediate Sagamore Lake (pH 6) exhibited cation and SO_4^{2-} dilution and a NO_3^- increase. Cation dilution also dominated events in relatively well buffered Djursvasslan stream in Sweden (Jacks et al. 1986) and Gem Lake in California (Stoddard 1987).

TABLE 3. Cumulative daily changes in major ions relative to alkalinity (dimensionless) in stream inflows and lake outflows during alkalinity depressions. Positive values denote contributions towards an alkalinity decrease and negative values denote contributions towards an alkalinity increase. The theoretical sum of the contributions (equal to Σdf_i) is 1.

	$\frac{\Sigma\Delta NO_3^-}{\Sigma\Delta alk}$	$\frac{\Sigma\Delta SO_4^{2-}}{\Sigma\Delta alk}$	$\frac{\Sigma\Delta A^-}{\Sigma\Delta alk}$	$\frac{\Sigma\Delta C_b}{\Sigma\Delta alk}$	$\frac{\Sigma(\Delta NO_3^- + \Delta SO_4^{2-} + \Delta A^- + \Delta C_b)}{\Sigma\Delta alk}$
1984					
HP0 No. 1	0.96	1.07	0.34	−2.92	−0.55
HP0 No. 2	−0.21	−1.87	−0.37	3.02	0.58
HP3	0.06	−0.33	−0.14	1.10	0.68
HP3A	0.77	−2.78	0.71	2.04	0.72
HP4	0.11	0.14	0.02	0.66	0.93
HP5	0.63	−0.74	−0.54	1.24	0.60
HP6 No. 1	0.10	−3.78	0.24	2.18	−1.26
HP6 No. 2	−0.55	−2.18	0.08	5.79	3.14
PC0	0.65	0.86	0.11	−2.55	−0.94
PC1	−0.39	−1.33	0.07	3.34	1.69
DE0	0.53	0.41	0.30	−2.24	−1.00
DE5 No. 1	−0.17	0.70	−3.40	1.01	−1.72
DE5 No. 2	−0.002	0.91	−2.15	1.13	−0.12
DE6	−1.55	0.09	0.16	8.38	7.08
DE10	0.85	−22.81	−6.10	26.89	−1.16
DE11	−0.24	−1.42	−0.01	2.59	0.92
1985					
HP0	0.41	0.28	−0.16	1.00	1.53
HP3	−0.09	−0.38	−0.31	1.94	1.16
HP4	−0.01	−0.32	−0.03	1.33	0.97
HP5	0.07	−0.09	−0.56	1.36	0.78
HP6	0.10	−1.35	0.002	0.40	−0.85
PC0	−0.23	−0.37	0.08	2.08	1.57
PC1 No. 1	−0.18	1.38	−0.66	0.45	1.00
PC1 No. 2	−0.10	−1.26	−0.77	2.74	0.61
DE0	0.20	−0.32	−0.08	0.90	0.70
DE6	0.03	1.84	−0.85	−0.60	0.42
1986					
HP3	−0.05	−0.27	0.03	0.99	0.70
HP4	−0.05	−0.06	−0.08	1.21	1.02
HP5	0.004	0.19	−0.23	0.87	0.83
HP6	0.11	−0.91	−0.01	0.57	−0.25
HP6A	0.10	0.45	−1.06	1.96	1.45
PC1 No. 1	−0.14	1.46	−0.73	−1.05	−0.45
PC1 No. 2	−0.27	1.48	−0.97	1.33	1.57
DE5	0.02	0.81	−1.04	0.50	0.28
DE6 No. 1	0.03	1.21	−1.11	−1.32	−1.20
DE6 No. 2	0.13	3.75	−4.16	−2.02	−2.30
DE8	0.08	−0.48	−4.12	1.02	−3.50
DE10	−0.05	3.70	−4.63	1.24	0.25
1984–86 (Mean ± SD)					
Harp	0.14 ± 0.36	−0.72 ± 1.24	−0.11 ± 0.38	1.37 ± 1.63	0.68 ± 0.98
Harp without HP6[a]	0.19 ± 0.36	−0.34 ± 0.97	−0.17 ± 0.42	1.13 ± 1.32	0.81 ± 0.49
Plastic	−0.09 ± 0.34	0.32 ± 1.28	−0.41 − 0.47	0.91 ± 2.11	0.72 ± 1.05
Dickie	−0.01 ± 0.54	−0.89 ± 6.75	−2.09 ± 2.15	2.88 ± 7.69	−0.10 ± 2.52

[a]HP6 excluded because of road salt inputs.

Log alkalinity in HP4 (pH>5.5) was highly correlated with log stream discharge in 1984 ($r^2 = 0.73$) and discharge episodes coincided closely with alkalinity depressions (Figs. 5 and 6). Dilution of cations in HP4 in 1977–82 was strongly coupled to peak discharge (Rustad et al. 1986). pH was also highly negatively correlated with discharge over a 12-mo period within each of four Pennsylvania streams (Sharpe et al. 1984). Baseflow pH was greater than 5.0 in the four streams. Maximum changes in H^+ and alkalinity in a circumneutral Pennsylvania stream during storm events during the growing season were best predicted by multiple linear regressions of hydrological parameters (Lynch et al. 1986).

In very acidic PC1 (pH <4.5), however, log |alkalinity| (all alkalinities were negative) was poorly correlated with log discharge in 1984 ($r^2 = 0.23$) (Fig. 6) and the major discharge events (B and C) on April 5 and April 19 produced only minor alkalinity depressions (Fig. 7). (The log–log correlation showed a slight dependence on the mathemetical transformation of the alkalinity argument, with r^2 for log (alkalinity +70) and log (alkalinity +200) versus log discharge being 0.15 and 0.20, respectively.) The alkalinity episode of February 14 to March 19, 1984, which coincided with discharge event A, was due primarily to C_b dilution (Fig. 8) with some anion dilution occurring (Table 3). During the April discharge events B and C, (Fig.

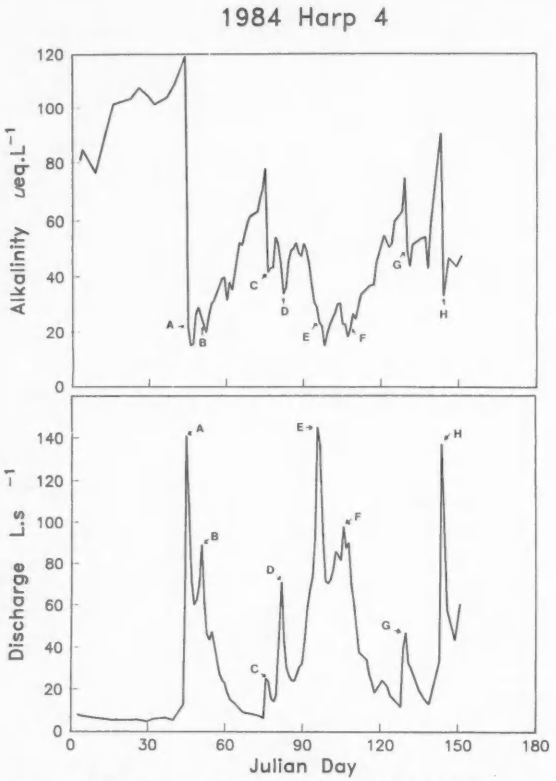

FIG. 5. Daily alkalinity and discharge in HP4 in 1984. Discharge events are labelled A–H.

7), dilution of SO_4^{2-} and C_b was considerably smaller resulting in smaller alkalinity changes (i.e. runoff was similar in composition to stream water). Hence, discharge may be a poor predictor of alkalinity depressions in very acidic streams and is consistent with the observation that dilution is less important.

It is clear that alkalinity depressions in streams occur over a wide range of background alkalinities. Therefore, episodic depressions in circumneutral streams are not necessarily precursors to chronic acidification.

Since atmospheric deposition rates of anions and cations are similar among the catchments, stream differences must be accounted for by catchment differences (Table 1). It is tempting to assume that differences among catchments are representative of changes within a given catchment over a longer time period as it becomes acidified.

In this spirit, the replacement of C_b dilution by anion increases during spring melt may be due partially to lower background C_b (i.e. there is less C_b to dilute) and due partially to higher export of anions. Catchment acidification may result in C_b export rates from catchments greater than their replacement by weathering which will eventually lower the background C_b and decreased anion retention during spring melt. The former is consistent with the decrease in the average cation concentration in Plastic Lake during a period of constant deposition (Dillon et al. 1987, 1988). The latter is consistent with SO_4^{2-} dilution in Harp inlets and increases in Plastic and Dickie inlets

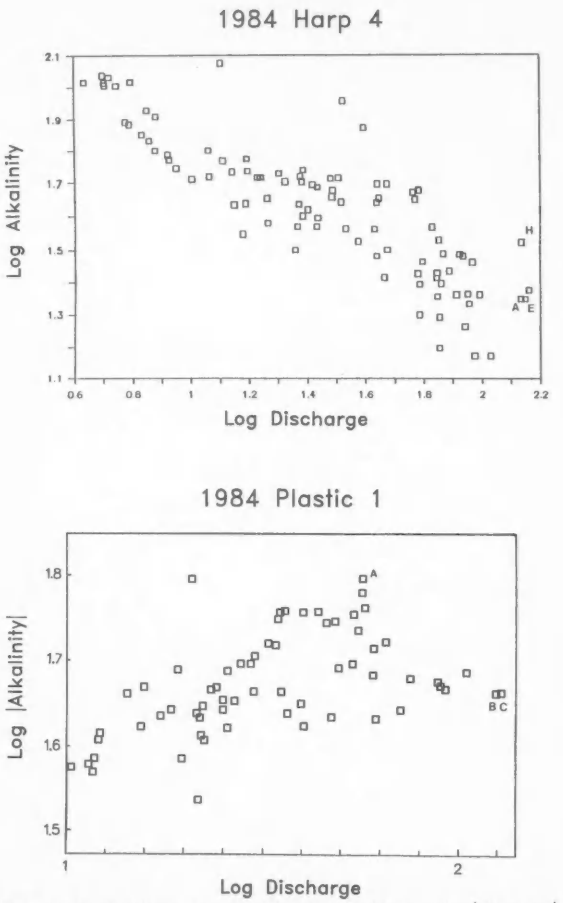

FIG. 6. Log alkalinity versus log discharge in HP4 and log |alkalinity| versus log discharge in PC1 in 1984. Absolute alkalinity values were used in PC1 because all alkalinities were negative.

(excluding DE10 in 1984) during spring melt. Long-term data bases are necessary for verification.

Speculation about the nature of catchment export/retention mechanisms responsible for stream behaviour is beyond the scope of this paper, particularly in light of the absence of detailed "on-shore" data. Successful development of a hydrogeochemical model integrating stream and catchment systems and capable of simulating short-term events will assist in the elucidication of these mechanisms (Hooper et al. 1988; Sverdrup and Warfvinge 1988). The present development of the "Birkenes" model has met with some success in predicting the behaviour of HP4 (Rustad et al. 1986).

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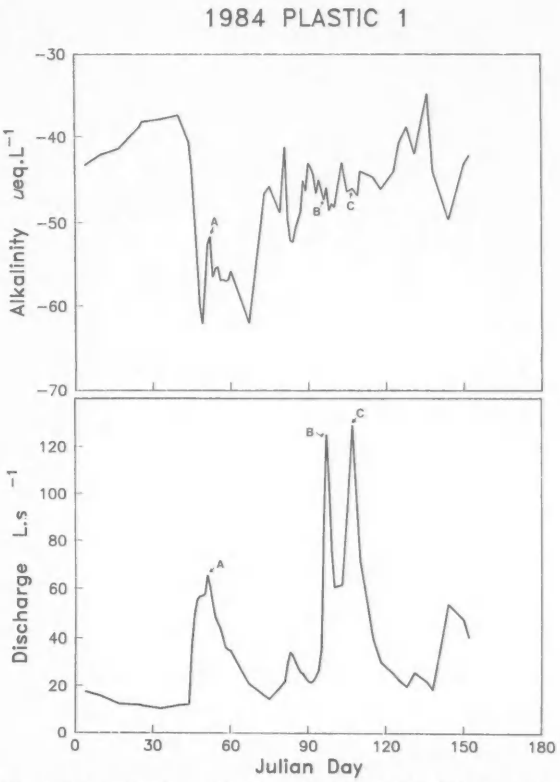

FIG. 7. Daily alkalinity and discharge in PC1 in 1984. Discharge events are labelled A–C.

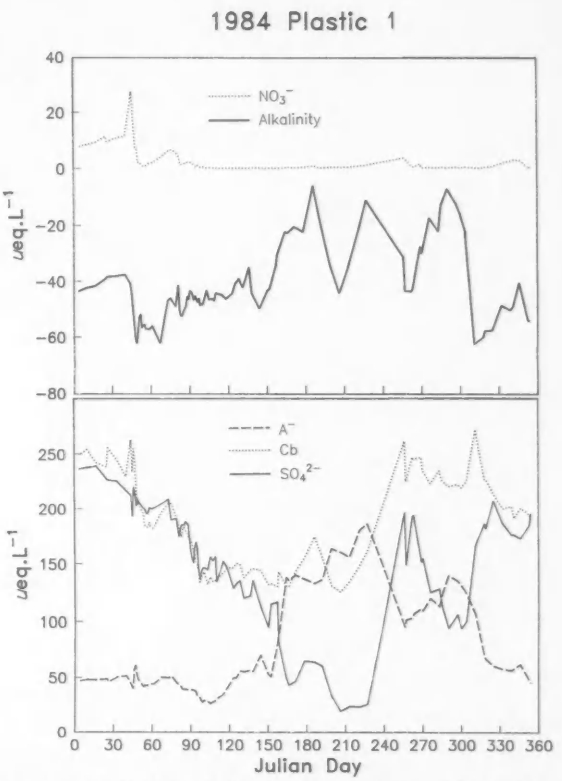

FIG. 8. Daily alkalinity, SO_4^{2-}, C_b, NO_3^-, and A^- in PC1 in 1984.

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Relationship between Chrysophyte Assemblages and Environmental Variables in Seventy-Two Sudbury Lakes as Examined by Canonical Correspondence Analysis (CCA)

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Dixit, S. S., A. S. Dixit, and J. P. Smol. 1989. Relationship between chrysophyte assemblages and environmental variables in seventy-two Sudbury lakes as examined by canonical correspondence analysis (CCA). Can. J. Fish. Aquat. Sci. 46: 1667–1676.

Relationship between surface sediment chrysophyte scales and limnological variables in 72 Sudbury lakes was examined using canonical correspondence analysis (CCA). CCA is a recently developed multivariate direct gradient analysis that has many advantages over indirect gradient analyses. Lakewater pH was identified as the most important variable influencing the distribution of scaled chrysophytes in Sudbury lakes. Almost all common chrysophyte taxa can be assigned a pH indicator value. In addition to pH, many chrysophyte taxa are sensitive to metal concentrations. A calibration model was developed to predict chrysophyte inferred pH using CCA. The model proved to be far superior to traditionally used models derived from multiple regression of pH indicator chyrsophyte assemblages. Applicability of the predictive pH equation was examined by reconstructing the recent pH history of Lohi Lake. The study provides compelling evidence that canonical correspondence analysis offers great promise in surface sediment calibration and pH reconstruction studies.

On a étudié la relation entre les écailles de chrysophytes des sédiments de surface et certaines variables limnologiques dans 72 lacs de Sudbury au moyen d'une analyse de correspondance canonique. Cette méthode d'analyse de gradient directe à variables multiples a été récemment mise au point : elle présente de nombreux avantages par comparaison à l'analyse de gradient indirecte. On a constaté que le pH de l'eau est la variable qui influe le plus sur la distribution des chrysophytes écailleuses dans les lacs de Sudbury. On peut attribuer une valeur indicatrice de pH à presque tous les taxons de chrysophytes communs. Par ailleurs, bon nombre de taxons sont non seulement sensibles au pH mais aussi à la concentration de métaux. On a mis au point un modèle d'étalonnage qui permet de prévoir le pH d'après l'étude des chrysophytes au moyen de l'ACC. Ce modèle s'est révélé supérieur à ceux habituellement employés jusqu'ici et dans lesquels les assemblages de chrysophytes indicateurs de pH font l'objet d'une régression multiple. Pour évaluer dans quelle mesure l'équation de prévision du pH est applicable, on s'en est servi pour reconstituer l'évolution récente du pH dans le lac Lohi. L'étude a apporté des résultats convaincants au sujet de l'analyse de correspondance canonique : cette méthode a beaucoup de potentiel pour l'étalonnage des sédiments superficiels et la reconstitution de l'évolution du pH.

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In the absence of historical limnological data, paleolimnologists have inferred past lakewater acidity changes using contemporary diatom and/or chrysophyte assemblages (Battarbee 1984; Charles 1984; Smol et al. 1986; Dixit et al. 1987, 1988a,b). However, inferred pH models used in these studies did not closely follow mathematical and ecological principles. This was because linear response models were often used, whilst it is generally believed that species respond to environmental gradients in a unimodal fashion (Jongman et al. 1987; Stevenson et al. 1989).

ter Braak and van Dam (1989) and Oksanen et al. (1988) discussed the usefulness of nonlinear models in inferred pH calibrations, and Stevenson et al. (1989) examined the potential of the recently developed canonical correspondence analysis (CCA) in developing predictive pH models. In community ecology, ter Braak (1986) introduced multivariate direct gradient analysis as an extension to weighted averaging ordination (correspondence analysis). Using CCA, axes are selected to be linear combinations of environmental variables, so that the species are related directly to a set of environmental variables. CCA has been used both for detecting species–environmental relationships and for tracing specific questions of species response to environmental variables (ter Braak 1987a). The advantages of using CCA over indirect gradient analysis techniques are discussed in detail in (Jongman et al. 1987).

Interpreting the relationship of algal microfossils with an environmental variable often raises the question: what is the significance of other variables to the established relationship? For example, it has been found that lakewater metal concentrations increase as a lake acidifies (Dillon et al. 1978; Norton et al. 1981; Nriagu et al. 1982). Dixit et al. (1988a, 1989a) indicated that, in addition to pH, chrysophytes appear to be sensitive to metal concentrations. In studies like these, CCA offers excellent potential for assessing the relative importance of multiple environmental variables on algal microfossil assemblages.

In this study we have applied CCA to examine the sensitivity of chrysophytes to the diverse limnological characteristics of

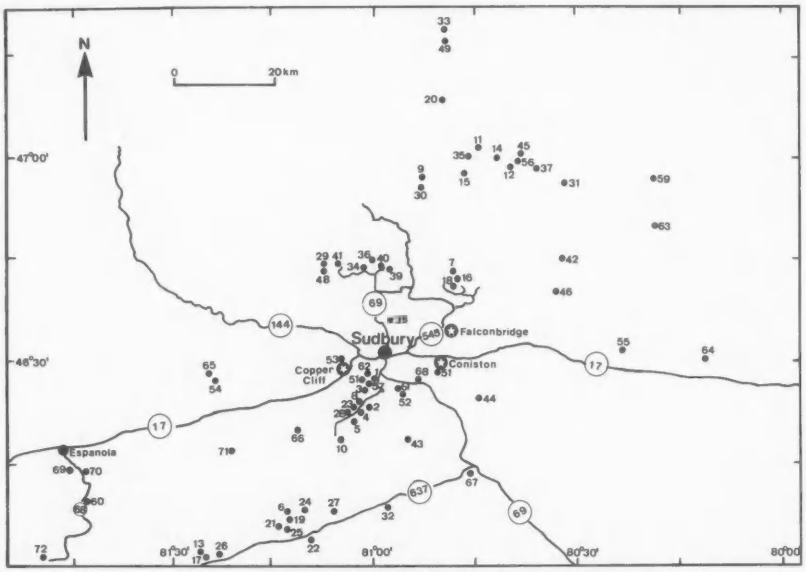

FIG. 1. Study area showing the location of the 72 study lakes.

72 Sudbury lakes. In addition to pH we were interested in examining the influence of metals on chrysophyte distribution because, if chrysophytes are influenced by variations in metal concentrations, these data will be required to fully exploit the usefulness of chrysophytes in paleo-environmental reconstructions. A predictive pH model was developed and tested to reconstruct the recent pH history of a poorly buffered Sudbury lake.

Study Area and Study Lakes

Seventy-two lakes located within 100 km of Sudbury were selected for this study (Fig. 1). Lakes were selected on the basis of their diverse pH and metal concentrations, which are influenced by variations in bedrock geology, prevailing wind patterns, and distance from metallurgical installations. Point sources in the Sudbury basin not only load the atmosphere with sulphur dioxide, but also contribute large amounts of metals such as Ni, Cu, Fe, and Se (Conroy 1974; Nriagu et al. 1982; Dixit et al. 1989a; Palmer et al. 1989). The northeast to southwest trend of the impact zone is related to prevailing wind patterns and geological sensitivity of the region. Regional geology is characterized by Precambrian metamorphic, plutonic, and volcanic silicate Canadian Shield rocks, overlain by thin Pleistocene glacial deposits. Lakes in the region are generally unproductive. Terrestrial vegetation ranges from deciduous and coniferous forests in the south to coniferous forests in the north. Selected limnological characteristics are presented in Table 1.

Materials and Methods

A short sediment core (about 30 cm long) was collected from or near the deepest point of the 72 study lakes using a modified Kajak–Brinkhurst (K–B) gravity corer. The surface sediment section (0 to 0.25 cm) of each core was carefully removed by extruding the core in a vertical position. An integrated water sample was collected from the deepest area of each lake. These samples were collected from the surface to the lower limit of the metalimnion in stratified lakes, and from the surface to 1 m above the sediment surface in unstratified lakes. Samples were analyzed for various limnological variables (Table 1) by the Ontario Ministry of the Environment and/or in our laboratory by using standard procedure (OME 1979, 1981; Dixit 1986).

Chrysophyte scales were recovered from sediment samples using an acid digestion technique (Dixit 1986) and slides were prepared by the Battarbee (1973) method. An attempt was made to count and identify a minimum of 500 scales for each sample; however, in 19 samples 86–200 scales were counted because scales were not common. Counting was carried out in random fields under oil immersion at 1250× magnification. In paleolimnological studies the counting of about 500 scales per sample is considered standard. Taxonomic references used were Takahashi (1978); Nicholls (1980, 1982, 1987, 1988); Wee (1982); Smol et al. (1984b); Asmund and Kristiansen (1986); and Dixit et al. (1988a). Although we attempted to split taxa identifications as much as possible, certain groups were problematic, and will require more detailed taxonomic study. Specifically, in this study, we attempted to distinguish *Mallomonas galeiformis* from *M. cristata* and *M. acaroides* v. *muskokana* from the nominate variety. In each case, two morphs appeared to be present in our samples, but we recognize this division as tentative.

Canonical correspondence analysis was performed using the CANOCO computer program (ter Braak 1987b). This program is designed to do a variety of multivariate analyses utilizing an iterative ordination algorithm. The environmental and species data are not required to be transformed. In the final analysis, some limnological variables (conductivity, alkalinity, Fe, Mn, Mg, K, total N, and elevation) were omitted due to their high variance inflation factors (VIF). ter Braak (1986, 1987b) clearly explained that a high VIF value occurs when a variable is almost perfectly correlated with other variables and thus has no unique contribution to regression equation. These variables are un-

TABLE 1. Selected limnological characteristics of 72 study lakes (Ontario Ministry of Environment, unpubl. data

Lake	pH	Cond. (μS/cm)	Alk. (μeq/L)	Cu (μg/L)	Ni (μg/L)	Pb (μg/L)	Zn (μg/L)	Fe (μg/L)	Mn (μg/L)	Al (μg/L)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)
1 Silver	4.15	330	−76.0	366	614	7	136	117	225	950	7.8	4.10	34.80
2 Pine	4.20	64	−68.0	120	350	31	36	380	150	630	3.6	0.64	0.74
3 Crooked	4.48	66	−34.0	110	420	13	11	160	170	170	4.6	1.50	1.74
4 Clearwater	4.49	76	−32.0	159	195	3	41	47	108	310	7.8	0.90	0.60
5 Unnamed 2	4.57	41	−20.0	53	160	7	25	76	200	320	3.1	0.56	0.82
6 Ruth-Roy	4.58	46	−26.0	3	16	2	21	51	92	511	2.1	0.30	0.60
7 M4	4.66	52	−20.0	29	190	11	41	80	190	260	4.0	1.26	0.86
8 Lohi	4.74	96	−18.0	60	186	3	42	49	96	169	5.6	1.10	1.60
9 Mountaintop	4.75	34	−15.8	8	18	8	100	130	88	480	1.9	0.52	0.74
10 Wavy	4.78	37	−14.6	18	75	1	6	76	150	180	2.7	0.78	0.82
11 Frederick	4.80	41	−15.0	4	11	1	20	100	180	190	2.8	0.68	0.66
12 Chiniguchi	4.87	38	−10.2	3	11	1	8	22	140	180	3.0	0.70	0.70
13 Acid	4.92	26	−7.8	2	7	23	57	49	170	250	1.5	0.52	0.44
14 Unnamed 1	4.94	34	−6.4	3	10	5	13	280	940	260	3.2	0.68	0.74
15 Telfer	4.95	38	−8.8	3	13	1	11	22	150	160	2.8	0.62	0.66
16 M1	5.08	51	−5.4	30	350	11	150	370	120	240	3.6	1.24	1.08
17 Lumsden	5.09	24	−1.6	11	38	28	51	150	220	240	1.5	0.48	0.42
18 M2	5.10	1100	−4.0	150	2000	12	110	21000	1500	5000	60.5	37.90	4.80
19 Johnnie	5.11	36	−8.0	5	19	1	14	99	105	140	3.1	1.00	0.70
20 Laundrie	5.51	28	11.8	2	2	1	4	17	32	74	2.3	0.64	0.66
21 Terry	5.55	53	16.0	8	21	1	16	126	46	650	1.3	1.20	0.70
22 Mahzenazing	5.55	39	10.0	4	23	2	12	132	90	91	1.9	1.20	1.05
23 Swan	5.63	56	5.8	11	80	5	11	520	100	19	5.5	0.92	1.56
24 Bell	5.64	33	11.6	3	11	1	3	59	80	64	3.0	0.88	0.82
25 Carlyle	5.65	43	8.0	2	12	1	15	39	68	110	2.3	1.00	1.05
26 George	5.73	31	8.4	0	4	3	0	76	130	54	2.5	0.82	0.70
27 Tyson	5.75	34	13.4	3	12	1	1	58	84	54	2.7	0.98	0.94
28 Tilton	5.76	54	6.2	18	92	1	11	75	68	34	5.2	1.20	1.60
29 Sans Chambre	5.79	53	18.0	4	15	2	15	146	55	71	4.6	0.90	0.75
30 Fraleck	6.02	32	26.6	3	3	1	5	60	27	59	2.7	0.78	0.84
31 Pedro	6.07	34	14.2	2	6	0	7	26	12	24	3.4	0.74	0.72
32 Attele	6.07	44	36.0	3	17	2	19	89	52	57	2.1	1.10	0.80
33 Whitepine	6.16	30	15.8	13	30	21	58	150	27	130	2.3	0.72	0.74
34 Pigeon	6.17	38	104.0	5	25	2	28	132	41	49	4.5	4.10	0.70
35 Alphretta	6.17	37	19.0	12	32	17	26	85	89	85	3.7	0.82	0.74
36 Joe	6.20	43	20.0	4	13	2	6	15	20	26	3.6	1.00	0.70
37 Laura	6.28	41	22.0	2	5	0	8	21	33	21	4.4	0.86	0.66
38 Whitson	6.42	122	42.0	4	7	4	9	120	38	37	5.8	1.98	11.20
39 Hanmer	6.42	37	31.4	7	25	0	19	43	34	23	3.8	0.78	0.80
40 Frenchman	6.43	35	28.0	6	19	5	21	34	19	42	3.4	0.80	0.80
41 Nelson	6.59	41	55.0	1	5	3	4	31	10	40	4.3	1.20	0.70
42 Kukagami	6.59	45	36.8	7	12	7	420	57	22	51	4.5	1.12	0.80
43 Horseshoe	6.66	48	80.8	17	36	20	25	320	18	210	6.0	25.2	6.38
44 S.E. Baby	6.69	39	50.8	18	57	4	59	210	28	76	3.4	1.22	1.08
45 Adelaide	6.69	39	53.4	2	4	5	12	48	34	41	4.2	0.86	0.76
46 Ashigami	6.72	42	61.4	—	—	—	—	—	—	—	—	—	—
47 Page	6.74	47	61.2	16	76	0	18	90	22	46	4.2	1.44	1.16
48 Labelle	6.78	37	108.6	4	10	7	12	240	38	73	3.7	0.94	1.14
49 Stull	6.80	38	69.6	2	2	10	15	43	12	61	3.2	0.94	0.92
50 Hannah	6.81	308	310.0	22	199	9	20	53	269	24	13.6	2.60	29.50
51 Baby	6.90	66	56.0	32	320	7	50	130	90	52	4.7	2.26	1.38
52 Raft	6.94	52	77.4	16	130	0	9	59	14	23	4.1	1.38	1.16
53 Clarabelle	6.97	340	86.8	96	2100	21	75	150	300	82	32.1	12.40	6.08
54 Skill	6.99	43	122.2	5	5	0	6	160	24	65	4.7	1.12	1.16
55 Ramer	7.00	66	195.8	6	6	0	4	200	20	110	6.1	2.12	2.44
56 Sawhorse	7.04	44	154.8	1	0	4	7	160	22	22	4.5	1.28	1.00
57 Middle	7.11	34	122.2	43	280	10	800	120	140	77	9.3	3.28	26.80
58 Little Round	7.15	82	166.2	24	110	6	28	180	46	71	7.0	2.50	2.80
59 Emerald	7.26	64	146.2	7	3	0	9	80	8	47	7.0	1.64	0.80
60 East Fox	7.26	332	243.0	1	2	1	2	56	12	10	19.6	4.40	3.00
61 McFarlane	7.35	269	580.0	10	62	2	11	47	10	38	18.4	6.10	22.30
62 Robinson	7.41	367	658.0	4	100	1	1	88	40	53	11.3	4.00	10.00
63 Wawashkesh	7.43	58	231.0	3	0	0	2	67	6	39	6.7	1.58	0.92
64 Deer	7.46	70	369.8	3	2	3	6	200	23	98	6.6	2.54	1.10
65 Fairbank	7.48	64	253.8	2	3	0	4	0	5	14	7.2	1.76	1.14
66 Round	7.50	104	241.8	11	43	0	5	59	8	21	8.4	2.80	5.74
67 Kakakiwaganda	7.59	89	251.0	6	11	20	25	89	12	51	4.0	1.86	1.44
68 Richard	7.62	174	334.0	3	147	1	1	34	14	23	15.1	4.90	4.10
69 Griffin	7.71	154	693.0	1	4	1	1	25	10	15	21.4	2.60	3.10
70 Anderson	7.81	97	452.0	1	5	1	1	95	15	25	13.7	6.60	6.10
71 Lit. Panache	7.83	97	537.6	3	4	0	2	58	12	21	11.4	2.50	2.68
72 Lewis	8.29	311	2310.0	1	1	2	1	76	20	7	27.6	5.00	3.36

bl. data, 1984; Dixit 1986; data collected in field 1987).

Na (mg/L)	K (mg/L)	Cl (mg/L)	SO_4 (mg/L)	Si (mg/L)	Color (TUC)	Tot.N (µg/L)	Tot.P (µg/L)	Secchi (m)	Depth (m)	Elev. (m)
34.80	1.22	38.60	39.1	1.7	1.0	128	3.5	7.0	12.0	288
0.74	0.41	0.35	17.2	0.5	1.0	59	4.0	4.8	8.0	300
1.74	0.75	3.65	19.1	2.4	2.5	106	7.0	4.8	8.5	273
0.60	0.36	5.50	20.6	1.5	0.0	36	5.0	10.0	21.0	283
0.82	0.31	0.30	12.2	0.4	0.5	80	5.0	7.0	12.0	300
0.60	0.36	0.50	10.3	0.3	5.6	440	5.6	9.5	18.0	288
0.86	0.37	0.30	16.6	0.5	10.0	80	4.2	9.5	13.0	300
1.60	0.70	5.80	20.2	1.2	4.2	78	6.6	5.5	19.0	280
0.74	0.20	0.15	10.6	1.8	3.0	230	8.6	4.0	9.0	362
0.82	0.36	0.30	9.6	1.4	3.0	138	5.9	7.0	37.0	261
0.66	0.32	0.35	13.3	0.4	0.0	98	3.0	10.0	13.0	360
0.70	0.31	0.25	12.7	0.6	0.0	90	4.0	9.0	35.0	313
0.44	0.21	0.20	7.9	0.9	0.0	68	4.0	11.3	14.0	315
0.74	0.28	0.25	10.5	1.6	19.5	130	5.0	2.2	10.0	318
0.66	0.28	0.25	12.5	0.5	0.5	110	3.0	14.0	23.0	314
1.08	0.37	0.30	16.9	1.1	9.0	91	3.3	3.5	5.0	318
0.42	0.20	0.20	7.6	1.0	0.0	110	5.0	8.5	17.0	238
4.80	5.00	0.85	455.0	13.0	7.5	39	25.5	3.0	10.0	318
0.70	0.38	0.50	10.8	0.9	6.7	81	4.5	6.0	28.0	242
0.66	0.27	0.25	7.3	0.8	14.0	186	5.0	5.0	8.5	390
0.70	0.40	0.50	11.6	0.8	—	130	16.3	2.0	9.0	242
1.05	0.52	1.40	10.2	1.1	14.1	225	13.0	3.5	18.0	194
1.56	0.43	7.15	10.5	0.5	13.5	166	4.2	4.0	7.0	285
0.82	0.45	0.35	8.1	1.0	9.5	200	5.0	3.5	32.0	225
1.05	0.52	0.60	8.8	0.5	7.1	196	12.0	5.0	12.0	209
0.70	0.37	0.45	9.8	1.0	1.5	110	4.0	14.0	22.0	186
0.94	0.47	0.45	9.0	1.4	8.5	210	6.0	4.5	22.0	207
1.60	0.50	3.70	12.8	0.1	2.5	54	7.8	6.0	12.0	257
0.75	0.40	0.50	14.3	0.7	5.4	336	16.1	8.5	15.0	349
0.84	0.34	0.25	9.9	1.8	10.0	180	4.0	5.0	145.	359
0.72	0.29	0.25	10.8	0.2	2.5	150	7.0	6.0	11.0	316
0.80	0.50	0.70	8.9	0.1	—	160	8.0	3.0	7.0	242
0.74	0.44	0.15	9.6	0.6	2.5	118	5.0	7.0	18.0	430
0.70	0.40	0.50	12.8	0.4	6.1	87	11.5	5.0	5.0	393
0.74	0.34	0.25	11.9	0.6	1.0	130	6.0	9.5	20.0	314
0.70	0.44	0.40	12.6	0.3	2.2	188	6.8	8.0	26.0	349
0.66	0.37	0.25	13.1	0.3	3.0	130	5.0	6.5	36.0	306
11.20	0.94	20.00	19.5	0.4	6.5	178	7.0	4.5	16.0	289
0.80	0.33	0.35	11.2	0.7	4.0	200	11.0	5.5	10.0	303
0.80	0.32	0.40	13.7	0.8	9.5	190	5.0	3.4	10.0	326
0.70	0.40	0.20	9.7	0.7	3.0	136	23.7	7.0	24.0	349
0.80	0.35	0.45	13.7	0.4	3.5	170	6.0	5.0	16.0	274
6.38	0.71	0.45	12.2	0.4	64.0	110	6.0	1.5	5.0	214
1.08	0.57	0.65	11.5	0.6	6.0	176	34.0	3.5	13.0	270
0.76	0.30	0.25	11.4	0.9	7.0	280	12.0	3.0	12.0	315
—	—	—	—	—	—	298	12.0	3.0	14.0	300
1.16	0.61	0.45	13.7	0.5	16.0	280	12.0	2.5	11.0	270
1.14	0.55	0.40	8.1	1.9	1.0	280	14.0	2.3	10.0	348
0.92	0.40	0.15	9.8	1.9	9.0	109	7.0	3.8	18.0	372
29.50	2.10	5.90	18.6	0.4	4.6	184	7.9	4.5	8.0	282
1.38	0.75	0.60	19.1	3.0	1.5	210	24.0	4.5	17.0	240
1.16	0.60	0.65	14.7	0.0	3.5	210	11.0	4.5	16.0	237
6.08	2.72	6.20	137.0	2.5	2.5	410	21.0	4.5	14.0	290
1.16	0.71	1.10	9.0	0.1	16.0	310	15.0	2.0	6.0	293
2.44	0.65	4.35	10.2	0.9	60.0	480	16.0	2.5	7.0	235
1.00	0.43	0.25	9.8	1.9	12.0	230	9.0	3.0	7.5	315
26.80	1.44	45.70	23.5	1.1	5.5	210	14.0	3.0	14.0	278
2.80	0.92	7.35	8.9	1.4	3.0	360	16.0	1.8	5.5	270
0.80	0.38	0.70	15.0	0.6	1.5	143	6.0	8.0	35.0	310
3.00	0.90	6.60	5.4	1.1	11.0	278	21.6	3.0	6.0	230
22.30	1.42	35.10	16.5	0.9	9.0	196	7.6	3.5	18.0	226
10.00	1.10	11.60	11.6	1.0	—	186	29.4	3.0	4.0	258
0.92	0.40	0.50	12.0	1.8	8.0	336	23.0	3.0	14.0	248
1.10	0.63	1.05	9.5	0.1	31.0	110	24.0	1.6	6.0	225
1.14	0.47	0.70	12.8	1.0	1.0	169	13.0	6.0	20.0	296
5.74	0.85	8.95	17.3	1.1	9.5	450	18.0	3.5	34.0	223
1.44	0.61	9.05	10.6	0.5	19.0	360	26.0	2.5	18.0	210
4.10	0.60	15.60	13.6	1.4	—	254	13.6	3.5	10.0	258
3.10	0.70	10.60	8.1	0.7	—	376	33.5	6.0	15.0	250
6.10	1.10	6.00	6.1	0.5	—	265	9.0	3.0	18.0	242
2.68	0.73	4.20	10.0	0.0	4.5	410	36.0	4.5	31.0	244
3.36	0.80	4.80	11.6	0.8	—	392	31.2	5.0	11.0	179

TABLE 2. Chrysophyte taxa identified in the surface sediment samples of 72 Sudbury lakes. The abundance weighted mean (AWM) pH and AWM Cu values of common taxa are also presented.

	AWM pH	AWM Cu (μg/L)
Chrysodidymus synuroideus Prowse	5.06	80.03
Chrysosphaerella brevispina Korsh. *em.* Harris *et* Bradley		
C. longispina Lasut. *em.* Nicholls	5.88	9.56
Mallomonas acaroides Perty *em.* Harris *et* Bradley	7.05	7.26
var. *muskokana* Nicholls	5.43	12.08
M. akrokomas Ruttner		
M. allorgei (Defl.) Conrad	6.42	8.59
M. caudata Inwanoff *em.* Krieger	6.66	6.57
M. crassisquama (Asmund) Fott	5.97	20.41
M. cf.*cristata* Dürrschmidt	6.41	6.58
M. cf. *cratis* Harris *et* Bradley		
M. cf. *dickii* Nicholls		
M. cf. *doignonii* Bourrelly		
M. elongata Reverdin	7.42	6.28
M. galeiformis Nicholls	6.30	16.14
M. hamata Asmund	5.68	5.82
M. hindonii Nicholls	5.02	6.86
M. heterospina Lund		
M. lelymene Harris *et* Bradley		
M. papillosa Harris *et* Bradley		
M. punctifera Korsh.	6.25	7.28
M. pugio Bradley		
M. pseudocoronata Prescott	7.18	12.15
M. transsylvanica Péterfi *et* Momeu		
M. tonsurata Teiling *em.* Krieger	7.63	6.27
Paraphysomonas spp.		
Spiniferomonas spp.		
Synura curtispina (Peterson *et* Hansen) Asmund	7.36	2.77
S. echinulata Korsh.	5.31	70.33
S. petersenii Korsh.	6.77	10.49
S. sphagnicola Korsh.	6.48	9.34
S. spinosa Korsh.	6.43	6.12
S. uvella Stein. *em.* Korsh.	6.49	10.76

stable and therefore have no interpretative value. Out of 33 chrysophyte taxa identified in the surface sediments (Table 2), 21 common taxa (>1% of the total scale counts in at least three lakes) were included in the analysis (Table 3).

Results and Discussion

Canonical correspondence analysis results can be displayed by an ordination diagram where environmental variables are depicted by arrows, and species and sites are marked by points. Although CCA generates separate environmental, species, and sample plots, which generally have different scaling, these plots can be presented as a single diagram by reconstructing them to the same physical length and then superimposing them with their axes aligned. In order to avoid presenting excessive data in one figure, we first examined the relationship between environmental parameters and chrysophytes by combining these two plots into a single biplot (Fig. 2).

In CCA, ordination axes are presented in sequence of variance explained by linear combinations of environmental variables. In our study, canonical axis 1 (38%) and axis 2 (16%) explained a significant amount of the variance in the species–environmental biplot (Fig. 2). The eigenvalue of axis 1 (0.37) and axis 2 (0.14) also indicates the importance of the first two axes in the ordination diagram. The eigenvalue for axes 3 and 4 was 0.13 and 0.11, respectively.

In the ordination diagram, environmental arrows point towards the maximum change of a parameter and arrow length indicates its importance in data interpretation (Fig. 2). The position of the environmental arrow depends on the eigenvalues of the axes and the intraset correlations of that environmental arrow (ter Braak 1986). The length of an arrow is equal to the rate of change in weighted average predicted from the biplot, and thus explains the extent of variation in species distribution along the parameter. Because long arrows correlate more strongly with ordination axes than short arrows, they have greater reliability in predictive applications.

A correlation matrix table outlines the relationship between various ordination axes and limnological variables (Table 4). In the ordination diagram the length of the pH arrow clearly indicates that lakewater pH was the most important variable in our data set (Fig. 2). pH was almost perfectly correlated with environmental axis 1 ($r=0.94$) and species axis 1 ($r=0.80$). Copper explained the next largest variation and was significantly related with axis 1 ($r=0.47$) and axis 2 ($r=0.53$). Arrows of other associated metals (i.e. Al, Ni, and Zn) also followed similar trajectories. The positioning of Cu and Al arrows indicated that they are inversely related to pH (Fig. 2).

TABLE 3. Percent abundance of 21 common chrysophyte taxa of study lakes. (See Table 2 for full genus and species identi

Lake	*C. long*	*M. allo*	*M. acar*	*M. cras*	*M. caud*	*M. cris*	*M. elon*	*M. hama*	*M. hind*	*M. gale*	*M. punc*	*M. pseu*	*M.* [illegible]
1 Silver	0.00	0.00	0.00	18.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2 Pine	0.00	0.00	0.00	21.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3 Crooked	0.00	0.00	0.00	32.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4 Clearwater	0.00	0.00	0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5 Unnamed 2	0.00	0.00	0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6 Ruth-Roy	0.00	0.00	0.00	78.00	0.00	0.00	0.00	7.90	1.90	0.00	0.00	0.00	0.00
7 M4	23.19	1.52	0.00	26.62	2.28	0.00	0.00	3.04	0.00	0.76	0.00	5.70	0.00
8 Lohi	0.00	0.00	0.00	63.59	0.00	0.00	0.00	0.18	0.00	0.09	0.00	0.46	0.00
9 Mountaintop	0.73	0.00	0.00	17.37	0.00	0.00	0.00	6.72	1.46	0.15	0.00	0.15	0.00
10 Wavy	0.95	0.00	0.00	90.51	0.63	0.00	0.00	0.63	0.00	0.95	0.00	1.27	0.00
11 Fredrick	2.30	0.00	0.00	38.60	0.00	0.00	0.00	17.30	3.80	2.60	0.00	0.00	0.00
12 Chiniguchi	4.04	0.00	0.31	28.15	0.62	0.00	0.00	20.22	1.56	0.31	0.00	0.00	0.00
13 Acid	1.95	0.00	0.00	41.40	1.46	0.00	0.00	7.95	38.64	0.81	0.32	0.00	0.00
14 Unnamed 1	32.40	0.00	0.00	16.74	7.08	0.00	0.00	6.87	2.15	0.43	0.00	0.00	0.00
15 Telfer	0.80	0.00	0.00	92.77	0.80	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.00
16 M1	0.47	0.00	0.00	83.07	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00
17 Lumsden	15.60	0.31	0.62	13.42	2.03	0.31	0.00	6.24	42.12	0.62	2.50	0.62	0.16
18 M2	0.00	0.00	0.17	45.98	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00
19 Johnnie	0.94	0.00	1.57	66.77	0.00	0.94	0.00	11.29	0.63	1.25	0.00	2.82	0.00
20 Laundrie	3.55	0.48	0.00	20.16	4.68	0.00	0.00	14.52	0.62	0.48	0.32	0.16	0.65
21 Terry	10.24	0.00	0.37	13.71	0.00	0.00	0.00	2.74	2.93	2.01	0.00	0.37	0.00
22 Mahezenazing	9.49	0.00	0.00	35.18	5.53	0.00	0.00	2.77	1.58	0.00	0.40	1.58	0.00
23 Swan	1.82	0.00	0.00	55.78	0.00	0.00	0.00	0.00	0.61	0.61	0.00	0.00	0.00
24 Bell	1.73	0.69	0.00	62.87	1.73	0.00	0.00	6.91	0.00	2.07	0.35	0.00	0.00
25 Carlyle	0.67	0.67	0.00	79.15	0.45	0.00	0.00	5.38	0.00	2.91	0.00	1.35	0.00
26 George	2.16	1.62	0.00	28.30	1.35	0.27	0.00	2.70	0.00	1.62	0.00	8.36	0.00
27 Tyson	0.00	0.65	0.00	72.55	1.96	0.00	0.00	0.65	0.00	11.76	0.00	7.19	0.00
28 Tilton	0.00	0.00	0.00	98.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29 Sans Chambre	20.18	0.00	6.12	54.13	5.50	0.00	0.00	4.59	0.31	3.67	0.92	1.22	0.00
30 Fraleck	19.96	1.02	0.20	25.05	5.09	1.43	0.00	4.89	0.00	2.24	1.43	2.04	0.20
31 Pedro	0.00	0.00	0.60	41.67	11.31	0.00	0.00	0.00	0.00	0.00	1.79	14.29	0.00
32 Attele	0.31	0.00	0.63	42.45	3.14	0.31	0.00	6.92	0.00	23.58	3.14	0.00	0.00
33 Whitepine	7.97	3.49	1.00	42.03	22.26	1.16	0.17	8.64	0.17	2.33	1.33	0.83	0.50
34 Pigeon	0.00	0.00	0.00	93.06	0.00	0.00	0.00	0.00	0.00	1.39	0.00	0.00	0.00
35 Alphretta	0.00	0.00	0.00	64.71	17.65	0.00	0.00	11.76	0.00	5.88	0.00	0.00	0.00
36 Joe	0.84	0.00	0.00	54.78	5.34	0.00	0.00	1.12	0.00	2.25	0.28	1.40	0.84
37 Laura	1.81	3.16	0.00	12.87	2.03	0.00	0.45	4.06	0.00	0.00	0.68	0.00	0.00
38 Whitson	0.88	0.00	0.00	3.74	3.52	0.00	0.00	0.00	0.00	0.22	0.00	0.88	0.22
39 Hanmer	0.91	0.00	0.00	55.45	34.09	0.00	0.00	2.73	0.00	0.91	0.00	0.00	0.00
40 Frenchmen	4.34	0.00	0.00	54.20	16.53	0.00	0.00	2.71	0.00	2.98	0.00	5.42	0.54
41 Nelson	0.81	1.63	0.81	85.37	0.81	0.00	0.00	0.81	0.00	0.81	0.00	1.63	0.00
42 Kukagami	5.71	2.86	0.00	51.43	14.29	0.00	0.00	5.71	0.00	0.00	1.43	10.00	0.00
43 Horseshoe	0.00	4.31	0.00	3.35	2.39	0.00	0.00	0.72	0.00	1.20	0.00	1.20	0.00
44 S.E. Baby	16.67	0.00	0.00	50.00	16.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
45 Adelaide	16.25	0.00	0.35	22.97	16.25	0.00	0.00	1.06	0.00	2.12	0.71	7.42	0.00
46 Ashigami	8.80	0.00	0.00	38.40	8.80	0.00	0.00	0.00	0.00	0.00	0.00	16.80	0.00
47 Page	0.17	0.00	0.00	20.70	4.47	0.00	0.00	0.66	0.00	0.83	0.00	0.83	0.00
48 Labelle	0.00	0.85	0.00	54.24	22.03	0.00	0.00	0.85	0.00	5.93	1.69	4.24	0.00
49 Stull	0.62	1.54	0.00	45.85	5.85	2.92	0.00	19.23	0.00	0.77	4.00	5.38	0.00
50 Hannah	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	96.00	0.00
51 Baby	0.43	0.00	0.00	41.29	1.51	0.00	0.65	0.22	0.00	0.86	0.00	26.02	7.31
52 Raft	0.00	0.00	0.00	80.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.38	0.00
53 Clarabelle	2.43	0.35	0.00	29.17	1.04	0.00	0.00	1.39	0.00	13.89	0.69	2.08	0.00
54 Skill	1.44	6.83	0.00	10.79	29.86	0.00	0.00	5.04	0.00	0.00	0.00	5.40	0.00
55 Ratter	0.00	0.00	0.00	39.42	11.54	0.00	0.00	0.00	0.00	0.00	0.00	8.65	0.00
56 Sawhorse	3.61	0.00	0.00	5.65	1.88	0.31	0.00	0.78	0.00	0.47	0.00	2.67	0.16
57 Middle	0.99	0.00	0.00	29.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	51.99	0.00
58 Little Round	6.48	0.00	0.00	11.11	5.56	0.93	0.00	0.93	0.00	0.00	0.00	74.07	0.00
59 Emerald	0.00	0.00	49.06	0.00	5.66	0.00	5.66	1.89	0.00	0.00	0.00	35.85	0.00
60 East Fox	0.00	0.00	0.00	37.04	23.46	0.00	0.00	1.23	0.00	0.00	0.00	3.70	0.00
61 McFarlane	0.00	0.00	23.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
62 Robinson	0.00	0.00	10.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	60.00	0.00
63 Wawashkesh	13.65	0.58	0.00	17.69	3.27	0.00	0.00	3.27	0.00	1.54	1.15	9.23	2.12
64 Deer	0.00	0.00	0.00	21.21	18.18	0.00	0.00	0.00	0.00	0.00	0.00	18.18	0.00
65 Fairbank	0.66	0.00	0.00	13.91	0.00	0.00	1.32	0.00	0.00	0.00	0.00	23.18	0.00
66 Round	2.22	0.37	0.37	11.85	0.37	0.00	0.00	0.37	0.00	0.37	0.00	16.67	0.00
67 Kakakiwaganda	0.99	0.16	0.00	18.59	1.48	0.66	0.66	0.00	0.00	0.00	0.00	27.24	4.77
68 Richard	0.00	0.00	0.00	6.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	93.68	0.00
69 Griffin	0.00	0.00	1.02	20.41	14.29	0.00	0.00	0.00	0.00	0.00	0.00	64.29	0.00
70 Anderson	0.00	0.00	0.00	65.17	2.49	0.00	0.00	0.00	0.00	2.98	0.00	6.47	0.00
71 Lit. Panache	0.00	0.00	0.00	1.43	15.71	0.00	4.29	0.00	0.00	7.14	0.00	14.29	54.28
72 Lewis	0.00	0.00	0.00	77.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00

es identification.)

M. tons	*S. echi*	*S. curt*	*C. synu*	*C. spin*	*S. spha*	*S. pete*	*S. uvel*	*M. acar musk*
0.00	81.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	71.43	0.00	7.14	0.00	0.00	0.00	0.00	0.00
0.00	62.10	0.00	0.00	0.00	0.00	0.00	0.00	4.71
0.00	48.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	11.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	22.81	0.00	0.00	0.00	2.28	6.46	4.18	1.14
0.00	30.32	0.00	4.79	0.09	0.46	0.00	0.00	0.00
0.00	71.53	0.00	0.00	0.00	0.15	0.29	0.00	0.00
0.00	4.43	0.00	0.00	0.00	0.32	0.00	0.00	0.00
0.00	22.60	0.00	0.00	0.00	4.70	6.80	0.00	2.30
0.00	19.91	0.00	0.00	0.31	6.22	9.64	0.31	0.00
0.00	4.87	0.00	0.00	0.65	0.49	0.81	0.00	0.00
0.00	3.22	0.00	0.00	0.00	5.15	4.29	0.00	21.24
0.00	0.80	0.00	0.00	0.00	0.00	3.21	0.00	0.00
0.00	15.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.16	10.61	0.00	0.16	0.62	0.16	1.25	0.00	0.00
0.00	45.98	0.00	7.52	0.00	0.00	0.00	0.00	0.00
0.00	12.54	0.00	0.00	0.00	0.00	0.00	0.94	0.00
0.65	40.65	0.00	0.00	0.81	0.00	0.00	0.00	8.32
0.00	36.01	0.00	5.12	0.00	22.30	3.66	0.00	0.00
0.00	0.00	0.40	0.40	0.40	5.53	27.67	1.58	2.37
0.00	23.40	0.00	0.00	0.00	17.48	0.00	0.00	0.00
0.00	15.89	0.00	0.00	0.00	1.73	1.90	1.73	2.07
0.00	0.00	1.35	1.12	4.26	0.45	0.00	0.00	2.02
0.00	27.76	0.00	2.16	0.00	0.00	21.56	0.00	0.00
0.00	2.61	0.00	0.00	0.00	1.31	1.31	0.00	0.00
0.00	1.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	6.12	0.00	0.00	0.61	0.92	0.00	0.00	0.00
0.20	2.85	0.20	0.20	0.81	9.37	20.37	1.22	0.20
0.00	4.76	2.38	0.00	23.21	0.00	0.00	0.00	0.00
0.00	10.38	0.00	0.63	0.94	0.94	0.00	5.03	0.00
0.50	2.99	0.00	0.17	0.17	0.00	2.49	0.17	0.00
0.00	2.78	0.00	0.00	0.00	0.00	2.78	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.84	10.96	0.84	0.28	3.93	1.12	12.92	0.00	0.00
0.00	4.51	3.39	0.00	26.19	0.00	29.80	0.00	9.48
0.22	47.91	0.00	0.00	0.00	0.00	40.22	0.00	0.00
0.00	1.82	0.00	0.00	0.00	0.00	0.00	1.82	0.00
0.54	2.71	0.00	0.00	3.25	0.00	4.07	0.00	2.44
0.00	4.88	0.00	0.81	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	1.43	7.14	0.00
0.00	23.45	0.00	0.48	26.56	1.67	31.58	3.11	0.00
0.00	16.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	7.07	0.00	0.00	2.83	7.42	13.78	1.06	0.00
0.00	3.20	0.00	0.00	2.40	1.60	10.40	4.80	1.60
0.00	1.66	0.00	0.00	0.33	0.00	69.54	0.17	0.50
0.00	3.39	0.00	0.00	0.00	5.08	0.00	1.69	0.00
0.00	0.92	0.00	0.00	0.46	0.00	10.92	1.54	0.00
0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
7.31	19.57	0.00	0.00	0.43	0.00	0.86	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00
0.00	18.40	0.00	0.00	0.00	12.15	12.15	2.08	0.00
0.00	7.91	1.08	0.00	1.80	0.00	25.90	3.96	0.00
0.00	28.85	0.00	0.00	0.96	1.92	7.69	0.00	0.00
0.16	0.31	0.16	0.00	1.73	78.49	3.14	0.47	0.00
0.00	0.00	0.00	0.00	0.00	0.00	17.22	0.00	0.00
0.00	0.93	0.00	0.00	0.00	0.00	13.02	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.89	0.00
0.00	23.46	0.00	0.00	4.94	1.23	0.00	4.94	0.00
0.00	0.00	0.00	0.00	0.00	0.00	76.92	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00
2.12	5.00	1.35	0.00	0.58	0.00	38.46	0.77	0.58
0.00	0.00	18.18	0.00	0.00	21.21	0.00	0.00	0.00
0.00	0.66	49.67	0.00	3.31	0.00	6.62	0.66	0.00
0.00	4.07	2.22	0.16	0.00	0.00	60.37	0.00	0.00
4.77	4.67	5.59	0.00	1.48	4.44	23.68	1.81	0.33
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	1.49	1.00	0.00	0.50	0.00	19.90	0.00	0.00
54.28	0.00	2.86	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

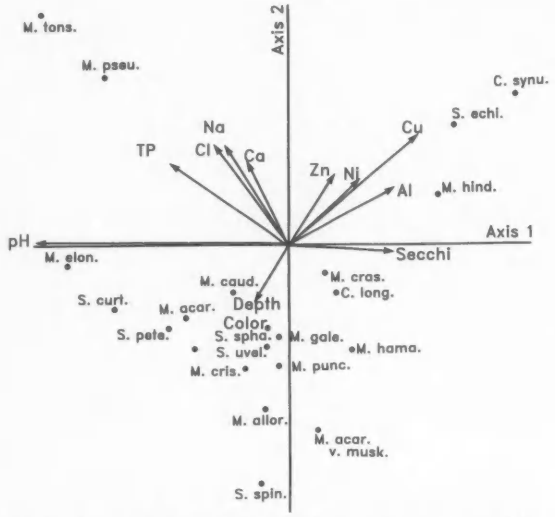

FIG. 2. CCA ordination biplot showing environmental variables (arrows) and chrysophyte species distribution (closed circles).

High metal concentrations in low pH Sudbury lakes have resulted from direct atmospheric deposition of metals, mobilization and subsequent input from the drainage basin, and leaching of metals from lake sediments (Nriagu et al. 1982; Chan et al. 1982; OME 1982).

Length of the total phosphorus (TP) arrow indicated that TP was also an important limnological variable in our lakes. Its direction suggested that high pH lakes also contain higher P levels. Arrows for Cl, Na, and Ca followed similar direction, but they were short. Although represented by a relatively short arrow, Secchi depth was inversely related to pH (Table 4). This conforms closely with the general observation of high Secchi transparency in clearwater acidic lakes (Almer et al. 1974; Wright and Gjessing 1976; Yan 1983). The identical positioning of the depth and color arrows indicate that deep lakes have higher color contents.

Lakes were also positioned in relation to the environmental variables (Fig. 3). Lake scores are the weighted mean species scores. Lakes positioned at the upper right have low pH and high metal concentrations, whereas lakes located at right but close to and below axis 1 have low pH and low metal concentrations. Similar results were also obtained for the majority of circumneutral and alkaline lakes positioned on the left of Fig. 3. In general the lakes located close to the TP arrow contained high P levels.

In the environmental–species biplot (Fig. 2), the position of various chrysophyte taxa followed the approximate value of the abundance weighted average of taxa with respect to any specific environmental variable (ter Braak 1987a). The weighted average approximates the optimum distribution of species along an environmental variable and variations in weighted averages among species define differences in their occurrence along that environmental variable (ter Braak and Looman 1986). Because pH and Cu were the two most important variables in our data set, we examined their influence on chrysophyte species distribution in detail. However, one can also examine the influence of other remaining variables, although the relationship would be weaker. Arrows representing pH and Cu were extended in both directions and a perpendicular line is drawn from each

TABLE 4. Weighted correlations between ordination axes and selected limnological variables.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	pH	Cu	Ni	Pb	Zn	Al	Ca	Na	Cl	SO_4	Si	Color	Tot.P	Secchi	Depth
SPEC AX1	1.00																						
SPEC AX2	−.15	1.00																					
SPEC AX3	−.03	.10	1.00																				
SPEC AX4	−.02	−.05	.02	1.00																			
ENVI AX1	.86	.00	.00	.00	1.00																		
ENVI AX2	.00	.67	.00	.00	.00	1.00																	
ENVI AX3	.00	.00	.58	.00	.00	.00	1.00																
ENVI AX4	.00	.00	.00	.58	.00	.00	.00	1.00															
pH	−.80	−.00	.04	.05	−.94	−.01	.07	.08	1.00														
Cu	.40	.35	−.04	.31	.47	.53	−.08	.53	−.44	1.00													
Ni	.21	.20	−.05	.16	.24	.30	−.08	.28	−.21	.56	1.00												
Pb	−.03	−.02	−.02	−.02	−.03	.32	−.12	−.04	.05	−.02	−.02	1.00											
Zn	.13	.21	−.07	.06	.15	.27	−.02	.22	−.12	.10	.09	−.03	1.00										
Al	.32	.18	−.01	.13	.38	.27	−.02	.22	−.40	.46	.66	−.02	.11	1.00									
Ca	−.13	.27	−.03	.14	−.15	.40	−.06	.24	.18	.29	.73	−.04	.00	.67	1.00								
Na	−.23	.37	−.25	.22	−.27	.55	−.44	.37	.11	.49	.22	−.03	.24	.09	.27	1.00							
Cl	−.23	.32	−.23	.24	−.27	.48	−.40	.41	.18	.42	.14	−.05	.30	.00	.24	.84	1.00						
SO_4	.18	.13	−.01	.13	.21	.19	−.01	.23	−.22	.39	.83	−.01	.06	.93	.81	.10	.02	1.00					
Si	.20	.16	−.07	.09	.24	.25	−.12	.16	−.24	.38	.72	−.04	.10	.90	.72	.06	.01	.92	1.00				
Color	−.10	−.18	−.11	.26	−.12	−.26	−.19	.45	.25	−.16	−.11	−.05	−.10	−.02	.02	−.01	−.03	−.04	−.06	1.00			
Tot.P	−.38	.30	.28	.03	−.41	.45	.48	.05	.52	−.10	.17	−.00	−.05	.10	.47	.01	.08	.21	.20	.13	1.00		
Secchi	.31	−.02	.09	−.29	.36	−.03	.15	−.50	−.46	.08	−.08	−.09	−.08	−.04	−.19	−.13	−.15	−.09	−.14	−.47	−.39	1.00	
Depth	−.10	−.16	.26	.01	−.12	−.24	.45	.02	−.04	−.11	−.13	−.03	−.11	−.11	−.12	−.12	−.06	−.08	−.09	−.32	−.12	.43	1.00

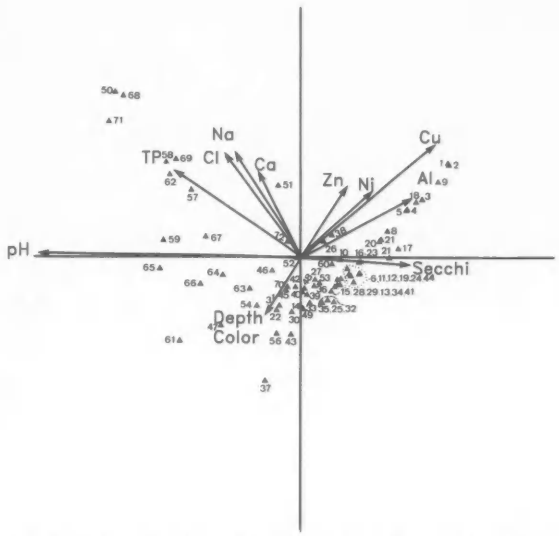

FIG. 3. CCA ordination biplot showing environmental variables (arrows) and coordinates of 72 study lakes (triangles).

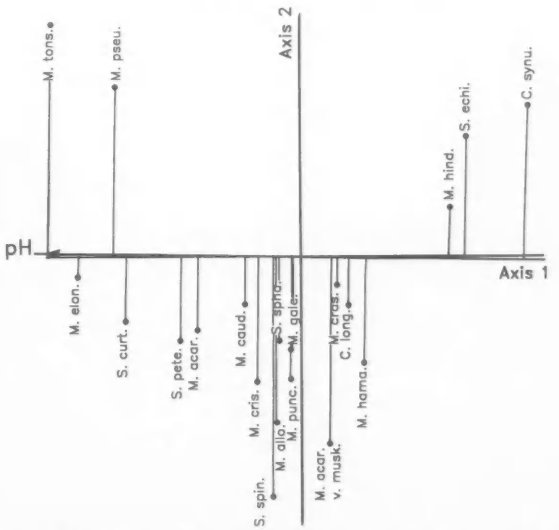

FIG. 4. Positioning of chrysophyte species along the pH arrow indicates the approximate ranking of the weighted averages of taxa with respect to pH.

species point to the arrows (Figs. 4 and 5). One can easily visualize the approximate ranking of the weighted averages of pH and Cu for chrysophyte taxa from the point where the perpendicular line intersects the arrow.

Figure 4 provides strong evidence that *Chrysodidymus synuroideus, Synura echinulata*, and *Mallomonas hindonii* occur in very acidic waters, whereas *M. hamata, Chrysosphaerella longispina, M. crassisquama*, and *M. acaroides* v. *muskokana* predominate in moderately acidic waters. Taxa such as *M. punctifera, M. galeiformis, M. allorgei*, and *M. caudata* predominantly occur in circumneutral waters. In alkaline lakes *M. pseudocoronata, S. curtispina, M. elongata*, and *M. tonsurata*

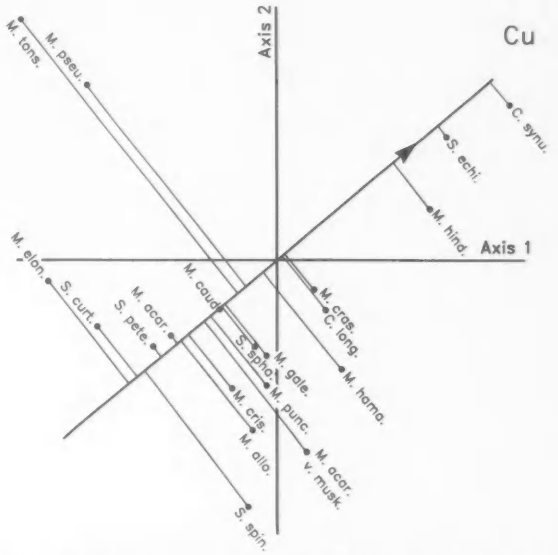

FIG. 5. Positioning of chrysophyte species along the Cu arrow indicates the approximate ranking of the weighted averages of taxa with respect to Cu.

are more competitive. Positioning of chrysophyte taxa on the pH arrow correspond closely to their pH indicator status reported in the literature (Smol et al. 1984a,b; Smol 1986; Charles and Smol 1988; Dixit et al. 1988a,b,1989a; Siver 1988a,b; Dixit and Dixit 1989). In Table 2 we have presented abundance weighted mean pH and Cu values of common chrysophyte taxa to facilitate future comparisons of species distributions among study regions.

Although the relationship was not as strong as observed with pH, the chrysophyte distributions are also related to concentrations of Cu and other associated metals (Figs. 2 and 5). For example, *Chrysodidymus synuroideus, S. echinulata*, and *M. hindonii* predominated in lakes that have high metal concentrations. *M. hamata, C. longispina, M. crassisquama*, and *M. pseudocoronata* occurred in lakes with intermediate metal concentrations, and taxa positioned at the lower left hand side (i.e. *M. elongata, S. curtispina, S. spinosa*, etc.) commonly occurred in lakes where metal concentrations were low.

An important characteristic of a CCA biplot is that one can easily visualize the influence of multiple environmental variables on species. We can identify that *C. synuroideus, S. echinulata*, and *M. hindonii* are metal tolerant acid water taxa, whereas *M. hamata, C. longispina, M. crassisquama*, and *M. acaroides* v. *muskokana* are metal sensitive acid water species. Similar metal related variation can also be established for circumneutral and alkaline pH indicator taxa. For example, *M. elongata, S. curtispina*, and *S. spinosa* have lower weighted means for Cu than does *M. pseudocoronata* (Fig. 5). It is possible that two taxa may have similar weighted means for one variable, but the values may differ widely for the other variable. For example, the pH indicator status of *M. acaroides* v. *muskokana* differed markedly from the nominate variety, but weighted means of Cu were similar.

The metal sensitivity of chrysophytes suggested by our CCA data confirms the calibration study of Dixit et al. (1988a) and other paleolimnological evidence (Dixit et al. 1989a). These

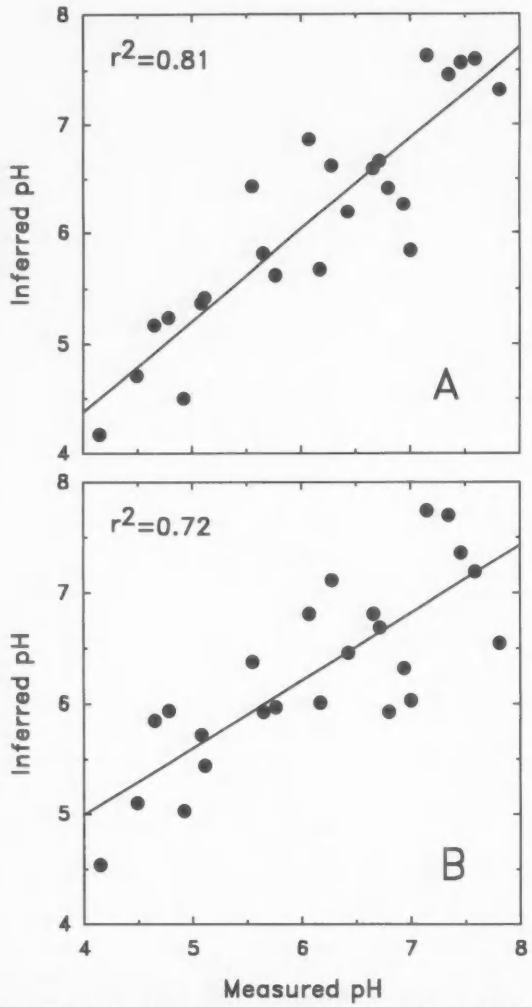

FIG. 6. Relationship between measured and chrysophyte inferred pH of 24 validation lakes. A = CCA calibration; B = multiple regression calibration of pH preference categories.

studies indicated that *M. hamata*, *M. acaroides* v. *muskokana*, and *M. crassisquama* were metal sensitive taxa, whereas *S. echinulata* and *C. synuroideus* are metal tolerant species. The metal tolerance of *M. hindonii* is further supported by Gibson et al. (1987), who found that the distribution of this taxon may have been positively related to total Al concentrations in an acidic lake. The combined pH-metal indicator status of *M. pseudocoronata* can be evaluated further from the stratigraphic study of Hannah Lake (Dixit et al. 1989a). In 1975, Hannah Lake was limed to increase its pH from 4.3 to 7.0 *Mallomonus pseudocoronata* was the only alkaliphilic chrysophyte that increased in dominance. Abundance of this taxon was not only related to an increase in pH, but may also have been influenced by the relatively high metal concentrations still present in this lake.

Because pH was identified as the most important variable influencing chrysophyte distribution, the next phase of this study was to develop a predictive pH model to reconstruct lake-water pH. Although not explored in this paper, predictive equations can be developed for other variables as well (e.g. Cu and P). To develop a predictive pH model, our 72 lake data set was first divided into two subsets. One subset included 48 calibration lakes and the other incorporated the remaining 24 lakes used for validating the calibration equation. The data set was reanalyzed, but calibration lakes were placed as active samples and validation lakes were included as passive samples. The active samples are those for which both species counts and measured pH values are included. Passive samples only contained chrysophyte counts. The passive samples do not influence the ordination, because their scores are computed afterwards (ter Braak 1987b). The approach we used is very similar to one employed by Stevenson et al. (1989). Based on our 48 active samples, the following calibration equation generated was:

$$\text{Inferred pH} = 6.207^{1} + \frac{(1.051^{2} \times \text{Axis 1 score}^{3})}{0.738^{4}},$$

where[1] = Mean measured pH of 48 calibration lakes,

[2] = standard deviation of the mean measured pH,

[3] = sample score based on chrysophyte species composition, and

[4] = canonical coefficient for pH. For further explanation of this equation see ter Braak (1987b), formula 7.21.

Reliability of this calibration equation was examined by computing the inferred pH of 24 validation lakes and comparing their inferred pH values with measured lakewater pH. Because these lakes were not included in the calibration equation, they objectively tested the accuracy of our predictive pH model. A simple linear regression analysis indicated that the relationship between chrysophyte inferred and measured pH is very strong ($r^2 = 0.81$; standard error = 0.25 pH unit). The relationship is not significantly different from 1.0 (Fig. 6a).

The pH predictive ability of our CCA model was compared with a multiple linear regression model (Dixit et al. 1988a; Charles and Smol 1988) where the inferred pH was parameterized by using the pH preference categories of chrysophytes against measured pH. Although the relationship between measured and inferred pH (Fig. 6b) was significant ($r^2 = 0.72$), the relationship between CCA inferred and measured pH was superior (Fig. 6a). In addition, the use of the CCA model is superior because it is unconstrained by the circularity in pH preference category models, i.e. predictive pH is close to measured pH, because the data used in the calibration equation and pH preference category assignments are the same.

While using CCA calibration, difficulties may occur if taxa that are rare or absent in the surface sediment calibration are common in deeper sediments. This may pose more difficulty in diatom calibrations (Stevenson et al. 1989), as it is not unusual to find a large number of diatom taxa in a single sediment sample. However, this may be less of a problem with chrysophytes because only a small number of taxa generally occur. For example, as opposed to 224 diatom taxa identified from the surface sediments of 30 Sudbury lakes (Dixit et al. 1988c), in the present study only 33 chrysophyte taxa were identified from 72 lakes. It is important to note that only common taxa are generally used in analysis. Because the total number of chrysophyte taxa identified is small, a majority can be incorporated in the calibration. Moreover, the taxa we considered rare have never been reported common in surface sediment and stratigraphic studies of chrysophytes (Smol et al. 1984a,b; Smol

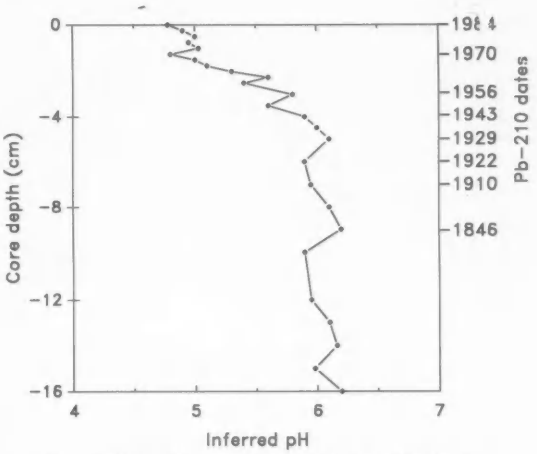

FIG. 7. Chrysophyte inferred pH history of Lohi Lake.

1986; Steinberg and Hartmann 1986; Dixit et al. 1988a,b, 1989a,b; Christie et al. 1988; Dixit and Dixit 1989).

After testing the predictive ability of chrysophytes on 24 test lakes, we developed a CCA calibration equation using all 72 lakes.

$$\text{Inferred pH} = 6.161 + \frac{(1.075 \times \text{Axis 1 score})}{0.697}.$$

Because this equation is based on a larger data set, the pH inferences derived from it should be ecologically more robust.

We further evaluated the usefulness of our CCA calibration by reconstructing the recent pH history of Lohi Lake. The lake is located 12 km southwest of Sudbury (Fig. 1), in an area where water quality has severely deteriorated (Conroy et al. 1974; Keller et al. 1980). Between 1973 and 1985 the lake was limed by the Ontario Ministry of the Environment (Yan and Dillon 1984). Stratigraphic changes in the chrysophyte taxa of Lohi Lake are discussed in Dixit et al. (1989a). Axis 1 scores of the core samples were obtained by placing them as passive samples in CCA and the inferred pH value for each of the 26 sediment levels was computed.

Our inferred pH profile indicates that Lohi Lake's pH has changed substantially in the past (Fig. 7). The background pH (pre ≈1930) of Lohi Lake ranged between 5.8 and 6.2, and the onset of the pH decline started in the 1930s. Lakewater pH declined from a high of ≈6.0 to its lowest value of 4.8 in 1984. The decline was most rapid between ≈1956 and ≈1970. The surface sediment inferred pH (4.8) corresponds closely with the measured lakewater pH (4.7) in 1984. Between 1970 and 1984 chrysophyte inferred pH slightly recovered, but not to the extent of increase in measured pH. In 1973 the lake was limed, and the pH was raised from 4.4 to 7.0 (Yan and Dillon 1984). The pH rapidly declined to 5.5 by mid-summer of 1974. In 1974 the pH was again raised to 6.5, but it again dropped to 5.5 by the spring of 1975. In 1975 the pH was raised for the last time to 6.7, but then gradually declined again to 4.7 by the fall of 1979. Chrysophyte species composition did not appear to respond to these short-term events. One possible reason for this is that lakewater pH continued to be somewhat depressed during spring of these years, when most chrysophytes tend to bloom. In contrast, in Hannah Lake where pH was raised and maintained (pH≈7) by liming, chrysophytes clearly tracked this manipulation (Dixit et al. 1989a).

Acidification in Lohi Lake primarily occurred from atmospheric deposition of SO_2. Although open pit roasting of sulphide-rich ore in the Sudbury basin began in the 1880's (ORF 1949), the pH decline only commenced after the installation of tall stacks in 1920s. Lakes which experienced acidification prior to the installation of stacks are those located in close proximity to smelters (Dixit et al. 1987). Timing of the pH decline in Lohi Lake corresponded closely to another nearby lake (Clearwater Lake) where diatoms inferred rapid acidification since 1930 (Dixit et al. 1987). Reduction in SO_2 emissions and installation of the Superstack in the early 1970's appear to have played an important role in cessation of any further pH decline in Lohi Lake after 1970. The pH of some Sudbury lakes has even recovered as a result of SO_2 emission declines (Dillon et al. 1986; Keller et al. 1986; Dixit et al. 1989b).

Conclusions

This study clearly demonstrates that CCA is a useful ecological ordination technique. CCA generates ordination biplots from which one can easily visualize and quantify the environmental factors determining species distributions. Sites or lakes can also be ordinated. Within our data set, pH was the most important variable regulating the distribution of chrysophytes. In addition to pH, many chrysophyte taxa are sensitive to metal contamination. Predictive models can be developed using CCA. In addition to closely following ecological and mathematical principles, CCA calibrations are appropriate for specific study regions because they are exclusively based on the relationship between contemporary microfossil assemblages and limnological variables. The close relationship between measured and inferred pH of 24 validation lakes provides additional evidence that our model reliably infers pH. As demonstrated with Lohi Lake, this approach will have wider applicability in reconstructing pH related changes in acid sensitive Sudbury lakes.

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Habitat Utilization by Juvenile Pacific Salmon (*Onchorynchus*) in the Glacial Taku River, Southeast Alaska

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Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, southeast Alaska. Can. J. Fish. Aquat. Sci. 46: 1677–1685.

Habitat utilization was determined in summer 1986 by sampling 54 sites of nine habitat types: main channels, backwaters, braids, channel edges, and sloughs in the river; and beaver ponds, terrace tributaries, tributary mouths, and upland sloughs on the valley floor. Physical characteristics were measured at all sites, and all habitats except main channels (current too swift for rearing salmon) were seined to determine fish density. Sockeye (*Oncorhynchus nerka*) averaged 23 fish/100 m^2, nearly twice the density of coho (*O. kisutch*) and four times that of chinook (*O. tshawytscha*), 14 and 6 fish/100 m^2, respectively. Sockeye were age 0, 27–84 mm fork length (FL), and most abundant in upland sloughs, beaver ponds, and tributary mouths. Coho were ages 0 and 1, 33–132 mm FL, and most abundant in beaver ponds and upland sloughs. Chinook were age 0, 40–93 mm FL, and more abundant than the other species in habitats with faster currents (1–20 cm/s), particularly channel edges. Each species was absent from about one-quarter of the seining sites of each habitat type. Thus, the lower Taku River provides important summer habitat for juvenile salmon, but many suitable areas were unoccupied, possibly because of their distance from spawning areas and poor access for colonizing fish.

En été 1986, pour connaître l'utilisation de l'habitat, on a échantillonné 54 points dans 9 types d'habitats : bras principaux, eaux dormantes, bras anastomosés, zones riveraines et portions marécageuses de la rivière ainsi qu'étangs de castors, tributaires de terrasse, embouchure de tributaires et marécages sur le fond de la vallée. On a mesuré les caractéristiques physiques à tous les points d'échantillonnage et l'on a senné tous les habitats, sauf les canaux principaux (où le courant est trop rapide pour l'élevage du saumon) afin de déterminer la densité de poissons. La densité moyenne de saumons rouges (*Oncorchynchus nerka*) était de 23 poissons/100 m^2 ce qui est à peu près le double de la densité de saumons coho (*O. kisutch*) et quatre fois la densité de saumons quinnat (*O. tshawytscha*) qui étaient respectivement de 14 et 6 poissons/100 m^2. Les saumons rouges étaient de la classe d'âge 0 et mesuraient 27–84 mm de longueur à la fourche (LF); ils étaient surtout abondants dans les marécages du fond de la vallée, les étangs de castors et à l'embouchure des tributaires. Les saumons coho étaient de classe d'âge 0 et 1, mesuraient 33–132 mm de LF et abondaient surtout dans les étangs de castors et les marécages du fond de la vallée. Enfin, les saumons quinnat étaient de classe d'âge 0, mesuraient 40–93 mm de LF et étaient plus nombreux que les autres dans les habitats où les courants sont plus rapides (1–20 cm/s), particulièrement dans les zones riveraines. Chacune des espèces était absente d'environ un quart des points de sennage dans les différents types d'habitats. Le cours inférieur de la rivière Taku est donc un habitat d'été important pour le saumon juvénile, mais un bon nombre de zones propices étaient inoccupées, peut-être parce qu'elles se trouvent à distance des eaux de fraye et qu'elles sont difficilement accessibles pour les poissons cherchant un milieu à coloniser.

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The glacial Taku River, which originates in British Columbia and flows through Southeast Alaska, is an important producer of Pacific salmon (*Oncorhynchus* spp.) for both United States and Canadian fisheries (Clark et al. 1986). The U.S./Canada Pacific Salmon Treaty establishes goals to manage the salmon stocks in such "transboundary" rivers for conservation, optimum production, and equitable sharing by the two countries (Natural Resources Consultants 1986). To accomplish these goals, information is needed on habitat utilization by juvenile salmon so that the stocks can be managed for maximum production from available habitat. Although chinook (*O. tshawytscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon are known to rear in the lower reaches of turbid Alaska rivers (Alaska Department of Fish and Game 1983; Wood et al. 1987; J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data), their use of this habitat is ill-defined. The purpose of this study was to determine patterns of habitat utilization by juvenile salmon in summer in the lower Taku River.

Study Area

The Taku River originates in northern British Columbia and flows through the Coast Range Mountains to Taku Inlet 40 km east of Juneau, Alaska (Fig. 1). The watershed is composed of 16 000 km^2, 95% of which is in Canada. Most of the year, the river is turbid with glacial silt. River flow is low (<100 m^3/s) in winter and high (>700 m^3/s) during snowmelt in June (Clark et al. 1986). Each summer, the lower river floods when ice dams impounding a lake on the Tulsequah River, 7 km upstream of the U.S./Canada border, suddenly break, sometimes tripling the river flow.

Five species of salmon occur in the drainage and are exploited by Canadian and Alaskan fisheries. Sockeye is the most numer-

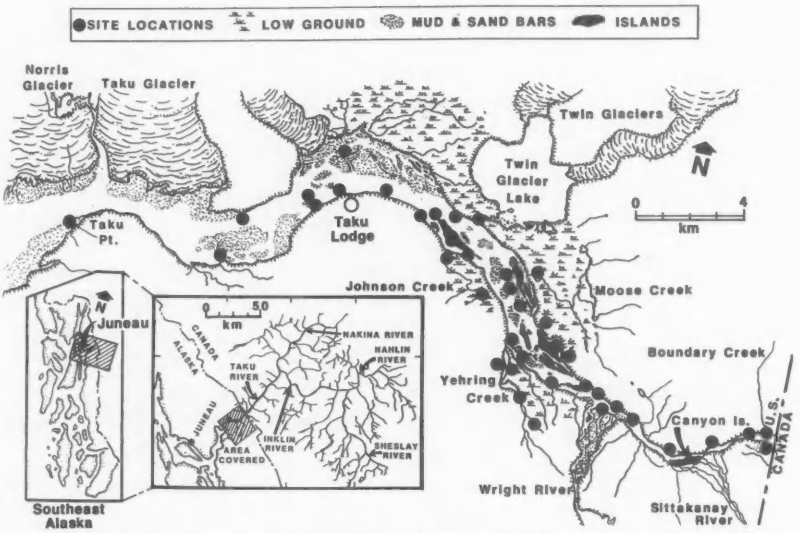

FIG. 1. Study area and locations of sampling sites in the lower Taku River, Southeast Alaska.

ous and valuable species in Taku River fisheries, with an annual harvest of about 100 000 fish (McPherson and McGregor 1986). Chinook stocks have been depressed and the fishery restricted since the 1970s. Annual adult returns of spring chinook recently have averaged 7500; in the 1950s, returns were typically about 25 000 (Kissner 1984). Adult returns of the other species are not well known, but are estimated to average 170 000 coho, 80 000 pink (*O. gorbuscha*), and 70 000 chum (*O. keta*) salmon (Alaska Department of Fish and Game, Commercial Fish Division, Juneau, unpubl. data).

This study was limited to the lower 28 km of the river between the river mouth at Taku Point and the U.S./Canada border, including off-channel areas on the valley floor (Fig. 1). In this area, the river flows within a wide (2–4 km), U-shaped glacial valley. The active river channel expands from 400 m wide at the border to nearly 3 km wide near the mouth. The river is extensively braided, and the substrate changes from mixed sand, gravel, and cobble near the border to mostly sand and silt near the mouth. Downstream of Taku Lodge, river height fluctuates 0–3 m daily during summer because of tidal influence as the river backs up during high tide; however, salt water does not intrude upstream beyond Taku Point.

Off-channel habitats on the valley floor consist of small, spring-fed streams often impounded by beaver dams, as well as tributary streams and rivers which drain valley slopes and flow across the valley floor to the river. Tributaries are glacial, humic (organic stain), or clear, depending on source and season. Sitka spruce (*Picea sitchensis*) and cottonwood (*Populus trichocarpa*) dominate high ground, and willow (*Salix* spp.) and red alder (*Alnus rubra*) flourish on low ground.

Methods

To determine habitat utilization by juvenile salmon, the habitat classification systems of Sedell et al. (1983); Alaska Department of Fish and Game (1983); and Edgington and Lynch (J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data) were adapted to classify habitat into two broad categories:

TABLE 1. Definitions of habitat types for classifying salmon rearing areas of the lower Taku River, Alaska.

Habitat type	Definition
River habitats	
Main channel	Area of main river flow; turbid, deep, turbulent, and rapid (>30 cm/s).
Braid	Shallow channel across mudflat or channel bar; water velocity moderate (10–30 cm/s).
Channel edge	Margin of main channels with moderate water velocity (<30 cm/s).
Slough	Slough formed when sediment and organic debris block the head of a braid or branch of a main channel. Water velocity varies from slow (0–15 cm/s) at low stage to rapid at high stage.
Backwater	Slack water formed by obstructions, such as a point bar in the main channel.
Off-channel habitats	
Terrace trib	Stream flowing across the valley floor to the river; may be glacial, humic, or clear.
Trib mouth	Lower reach of a tributary affected by the river; often has slack water.
Beaver pond	Terrace tributary impounded by beaver dam.
Upland slough	A slough fed by spring or terrace tributary; has outlet to the river.

(1) river habitats within the active river channel, and (2) off-channel habitats on the valley floor. Each category was divided further according to water velocity regime, for a total of five river habitats and four off-channel habitats (Table 1). A total of 54 sites (3 to 17 of each type) were selected to give a representative sample of available habitat. Each site was sampled once between 8 July and 18 September 1986. Habitat types were sampled in random order to eliminate temporal bias. All habitat types except main channels were sampled for both habitat characteristics and fish density.

To describe habitat, selected physical characteristics were measured at each site. Water depth (measured with a meter stick) and velocity (measured at mid-depth with a current meter) were measured at one-quarter, one-half, and three-quarters across the

middle of each station; pieces of large woody debris (>10 cm diameter) were counted; and water temperature was taken. Turbidity of a water sample from each site was determined to the nearest 50 Jackson turbidity units (JTU) by titrating a standard suspension into distilled water and comparing it with the sample (American Public Health Association 1971).

To estimate fish density, at least three separate stations spaced 50 m apart at each of 49 sites were seined for fish. Main channels, except for channel edges, were assumed too swift (mean, 102 cm/s) to contain rearing salmon (Hillman et al. 1987) and were not seined. Where water was too deep to wade (beaver ponds, sloughs, and tributary mouths), a beach seine (15.2 m long, 2 m deep, 6-mm mesh) was set from a boat and retrieved from shore; the area seined was 37 m^2. Where water was shallow enough to wade (channel edges, braids, backwaters, and terrace tributaries), a pole seine (3 m long, 1.2 m deep, 6-mm mesh, and fixed with a pole at each end) was pulled against the current parallel to shore for 20 m; the area sampled was 54 m^2. Stations with woody debris were seined by working the net around the debris; however, seining probably was less effective in dense debris than in other areas.

The number of fish at each station was estimated by the removal method (Zippin 1958), based on at least three passes with a seine. The removal method minimized bias from using different capture methods in the different habitat types. During sampling, probability of capture was assumed constant, and immigration and emigration were assumed negligible. Salmon probably did not avoid the seine in most areas because of turbidity. Population estimates were divided by the area seined to compute density, and density at each site ws computed as the mean at the stations. Fish were anesthetized with MS-222, identified to species, counted, and measured for fork length (FL). Scales were taken from up to 25 fish of each species to determine age: age-0 fish were young-of-the-year, and age-1 fish had one winter annulus. After sampling, fish were released where they had been captured.

Overlap in habitat use (Horn 1966) between salmon species was calculated as

$$C = \frac{2\sum_{i=1}^{n} X_i Y_i}{\sum_{i=1}^{n} X_i^2 + \sum_{i=1}^{n} Y_i^2}$$

where C is overlap and X_i and Y_i are catches of species X and Y from habitat type i of the n habitat types, as a proportion of the total catches in all samples. Overlap ranges from 0 (complete segregation) to 1 (complete overlap), and values greater than 0.6 are considered significant (Zaret and Rand 1971).

Total populations of juvenile salmon in the area of the lower river between Taku Point and the U.S./Canada border were estimated from the mean fish densities and total area of each habitat type in the lower river. Area of habitats was measured with a computer by digitizing outlines of habitats drawn on aerial photographs (Fig. 2; U.S. Department of Agriculture, Agricultural Stabilization and Conservation Service, August 1977; scale, 1:6272). Area of channel edges was computed from the length of main channels by assuming an average edge width of 3 m. This edge width approximated the area of reduced current in most channels and equalled the length of the net used to sample fish. Confidence limits for total populations were computed from the variance for the stratified population mean (Cochran 1953). To determine degrees of freedom, the number of potential sites was computed for each habitat type by dividing its total area by the mean area sampled in the sites of that type.

Results

Sockeye, coho, and chinook were the most abundant salmonids. Overall sockeye density at 49 sites averaged 23 fish/100 m^2, nearly twice the density of coho (14 fish/100 m^2) and four times that of chinook (6 fish/100 m^2). Dolly Varden (*Salvelinus malma*) also were captured, but in low mean density (<1 fish/100 m^2). A few chum salmon, steelhead trout (*O. mykiss*) and cutthroat trout (*O. clarki*) also were caught, and sculpins (*Cottus* spp.), sticklebacks (*Gasterosteus aculeatus*), and whitefish (*Prosopium* spp.) sometimes were abundant, but numbers were not analyzed.

Salmon Size and Age

Sockeye and chinook were predominantly (99%) age 0, and ranged from 27 to 84 mm and 40 to 93 mm FL, respectively; coho were mixed ages 0 and 1, and ranged from 33 to 132 mm FL (Fig. 3). Age composition of coho differed between beaver ponds and other habitats: beaver ponds averaged 89% age 1, and other habitats averaged 96% age 0. Length frequency distributions of sockeye, chinook, and age-1 coho were approximately normal, whereas that of age-0 coho was highly skewed, with a concentration in the smallest length classes.

Mean FL increased during the study period, indicating apparent growth (Fig. 4). From early July to mid-September, sockeye mean FL increased 0.25 mm/d, from 40 to 58 mm; age-0 coho mean FL increased 0.14 mm/d, from 39 to 49 mm; and chinook mean FL increased 0.15 mm/d, from 55 to 66 mm. Except for some beaver ponds, all habitat types had similar mean FL. In beaver ponds in the south-facing Sockeye Creek drainage (Fig. 1), sockeye and age-0 coho were significantly ($P<0.025$; t-test) larger than expected, based on the regression equations, probably because of warmer water in the ponds (Table 2). The regression of chinook mean FL on date had more variation and a lower R^2 than that of the other species. Some of this variation was caused by a trend in chinook size with location in the river. Chinook mean FL was negatively correlated ($r=-0.67$; $P<0.01$) with distance from the river mouth and decreased from 70 mm in the tide-influence zone to 62 mm at the U.S./Canada border (Fig. 5).

Habitat Utilization

Physical characteristics of the sites differed significantly ($P<0.05$; Kruskal–Wallis test) between habitat types (Table 2). Mean water velocity was lowest (0–5 cm/s) in sloughs, backwaters, tributary mouths, upland sloughs, and beaver ponds; intermediate (10–21 cm/s) in braids, channel edges, and terrace tributaries; and highest (102 cm/s) in main channels. Mean depth ranged from 0.3 m in braids to 1.0 m in beaver ponds and 2.9 m in main channels. Typically, river habitats were turbid (means, 240–400 JTU), whereas off-channel habitats were clear or humic (means, 20–208 JTU). Large woody debris was common in terrace tributaries but absent from upland sloughs. Water temperature was 2–4°C higher in beaver ponds and upland sloughs than in channel edges, braids, and terrace tributaries. Temperature of channel edges and braids was not significantly correlated with distance from Taku Point ($r=0.22$; $P=0.13$;

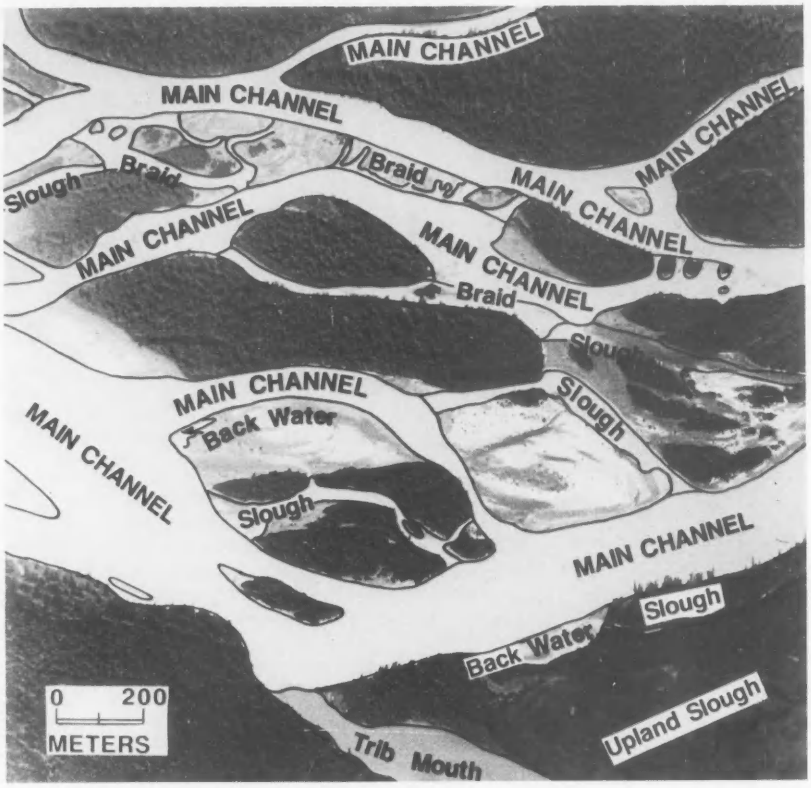

FIG. 2. Example of an aerial photograph of a section of the lower Taku River, with habitat types delineated.

from Taku Point ($r = 0.22$; $P = 0.13$; $n = 28$); thus, temperature did not change longitudinally along the river.

Distribution of salmon was most closely related to water velocity, and turbidity had a secondary influence. Sockeye and coho occupied significantly ($P < 0.05$; Kolmogorov–Smirnov test) slower current than chinook (Fig. 6). Sockeye and coho densities were highest in still or slow water (≤10 cm/s), whereas chinook density was highest in slow-to-moderate current (1–20 cm/s). All species were virtually absent from areas with currents greater than 30 cm/s. Correlations (r) between fish densities and turbidity in all 49 sites were weak: 0.14 ($P = 0.16$) for chinook, −0.24 ($P = 0.05$) for sockeye, and −0.32 ($P = 0.01$) for coho. Differences in water velocity may have masked effects of turbidity. For sites with suitable water velocity (≤10 cm/s for sockeye and coho and 1–20 cm/s for chinook, based on relationships in Fig. 6), both sockeye and coho had significantly ($P < 0.01$; Kruskal–Wallis test) lower density in highly turbid (≥400 JTU) than in less turbid water (Fig. 7). Chinook density, however, was similar ($P > 0.05$) in areas of different turbidity.

Mean salmon density in the habitat types corresponded to water velocity but also differed between the river and off-channel areas (Fig. 8). Sockeye were most abundant (means, 36–73 fish/100 m^2) in sloughs in the river and tributary mouths, beaver ponds, and upland sloughs off channel — all habitats with mean water velocity less than 10 cm/s (Table 2). Coho almost exclusively occupied off-channel habitats with slow water; the highest mean densities were in beaver ponds and upland sloughs (58–59 fish/100 m^2). Coho were consistently scarce (means, 1–3 fish/100 m^2) in river habitats, even those with slow water. Chinook primarily were in river habitats, particularly sloughs and channel edges (means, 6–8 fish/100 m^2), and off-channel terrace tributaries and tributary mouths (means, 5–8 fish/100 m^2) — all habitats with mean water velocity 3–15 cm/s. Chinook were virtually absent (mean, <1 fish/100 m^2) from beaver ponds and upland sloughs. Differences in density between habitat types were significant ($P < 0.05$; $N = 49$; Kruskal–Wallis test) for coho and chinook but not for sockeye ($P = 0.35$) because sockeye were absent from several beaver ponds and upland sloughs.

Each species was present in only about three-quarters of the sites, and even the most suitable habitat often was unoccupied (Fig. 8). Sockeye, for example, were absent from one-half of the beaver ponds and one-quarter of the upland sloughs, yet density exceeded 150 fish/100 m^2 in some of these habitats. Maximum density within a habitat type, a measure of habitat suitability, was unrelated to occurrence of a species in the habitat. Habitat types with extremely low maximum density (≤5 fish/100 m^2) had low percent frequency of occurrence (%FO), but in others, %FO averaged 74% and was not correlated ($r = 0.00$) with maximum density (i.e. unrelated to suitability).

Overlap (C) in habitat use was high (0.80) between sockeye and coho, moderate (0.38) between sockeye and chinook, and low (0.18) between coho and chinook. Mean densities of sock-

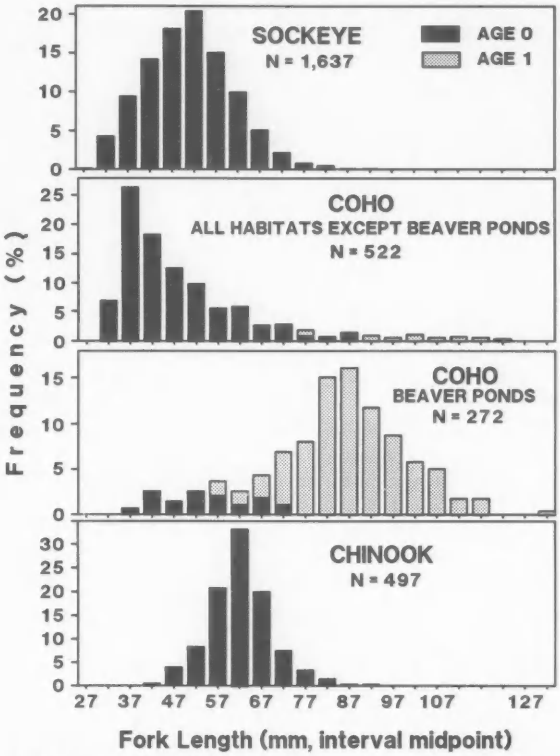

FIG. 3. Frequencies of fork length (in 5-mm intervals) and age classes of juvenile sockeye, coho, and chinook salmon from the lower Taku River, Alaska, July–September 1986.

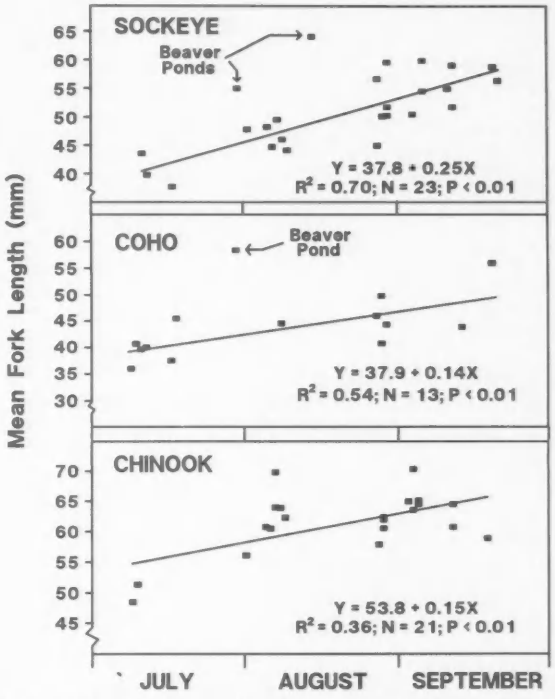

FIG. 4. Mean length of age-0 sockeye, coho, and chinook salmon in the lower Taku River, Alaska, July–September 1986. Regression equations relate mean FL (Y) to number of days (X); day 1 = July 1. Data are from sites with at least six FL measurements. The three labeled points representing beaver ponds were outliers and were not used in the regressions.

eye and coho in the habitat types also were positively correlated (rank correlation $r_s = 0.83$; $P < 0.01$; $n = 8$), whereas coho and chinook were negatively correlated ($r_s = -0.75$; $P < 0.05$). Both sockeye and coho were abundant in upland sloughs, beaver ponds, and tributary mouths; however, sockeye were less abundant in terrace tributaries and more abundant in sloughs and backwaters than were coho. Coho and chinook generally occupied different habitats, with the exception that both species occurred in moderate density in terrace tributaries and tributary mouths. Each species, however, occurred independently of the others ($P > 0.50$; Chi-square test; $n = 49$). Presence of coho at a site, for example, did not influence occurrence of sockeye and chinook.

Total wetted area of the lower Taku River and its off-channel habitats was 1932 ha and consisted mostly of main channels and braids (Table 3). Main channels, which were too swift for rearing salmon, comprised 70% of the area, and braids, which were marginal habitat, comprised 21% of the area. All other river habitats were only 4% of the area, and all off-channel habitats were only 5% of the area. Because of the large area of braids, the greatest number of sockeye and chinook were in this habitat, even though mean density in braids was low. The habitats with highest mean densities, however, were only a small part of the total area. Tributary mouths and beaver ponds, for example, were only 2.2% of the area but accounted for 52% of the coho. Estimated total populations were 641 000 sockeye; 293 000 coho; and 248 000 chinook, for a total of 1 million salmon of the three species. Because of a large variance in

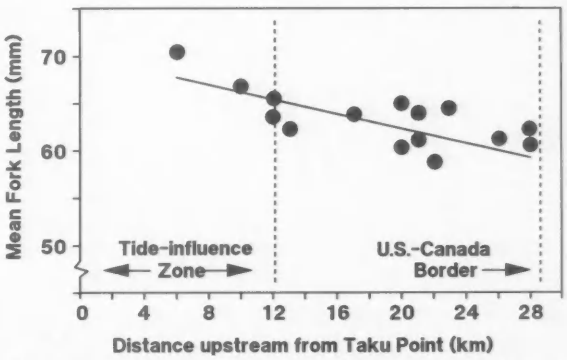

FIG. 5. Longitudinal trend in mean fork length of juvenile chinook salmon in channel-edge and braid habitats in the lower Taku River, Alaska, July–September 1986. Data are from sites with at least six FL measurements.

salmon density within habitat types, the 95% confidence intervals were wider than ±50% of the estimated total populations.

Discussion

Fish Density

The results indicate that the lower Taku River and associated

TABLE 2. Mean physical characteristics of habitat types in the lower Taku River, Alaska, summer 1986. Habitat types are defined in Table 1. Ranges are in parentheses.

	River habitats					Off-channel habitats			
	Main channel	Braid	Channel edge	Slough	Backwater	Terrace tributary	Tributary mouth	Beaver pond	Upland slough
Number of sites	5	5	17	5	3	5	6	4	4
Water velocity (cm/s)	102 (30–240)	19 (10–27)	11 (3–30)	3 (0–16)	1 (0–1)	15 (11–20)	5 (0–15)	0 (0–1)	1 (0–2)
Water depth (m)	2.9 (1.6–3.8)	0.3 (0.2–0.5)	0.4 (0.2–0.6)	0.5 (0.3–0.7)	0.6 (0.4–0.7)	0.5 (0.4–0.7)	0.8 (0.2–1.2)	1.0 (0.6–1.4)	0.9 (0.2–1.4)
Turbidity (JTU[a])	400 (400–400)	400 (400–400)	383 (100–600)	240 (0–400)	400 (400–400)	20 (0–100)	208 (0–400)	25 (0–100)	150 (0–300)
LWD[b] (No./station)	0.07 (0.0–1.0)	0.07 (0.0–0.3)	0.17 (0.0–1.0)	0.13 (0.0–0.7)	0.17 (0.0–0.5)	0.27 (0.1–1.0)	0.06 (0.0–0.3)	0.08 (0.0–0.7)	0.00 (0.0–0.0)
Water temperature (°C)	8.0 (4.6–9.8)	8.7 (7.2–10.7)	7.9 (4.6–9.7)	10.3 (7.9–11.9)	9.5 (8.3–10.6)	9.1 (8.3–11.2)	9.5 (6.9–12.8)	12.0 (9.5–15.4)	11.4 (9.4–16.2)

[a]Jackson turbidity units.
[b]Large wood debris (>10 cm diameter).

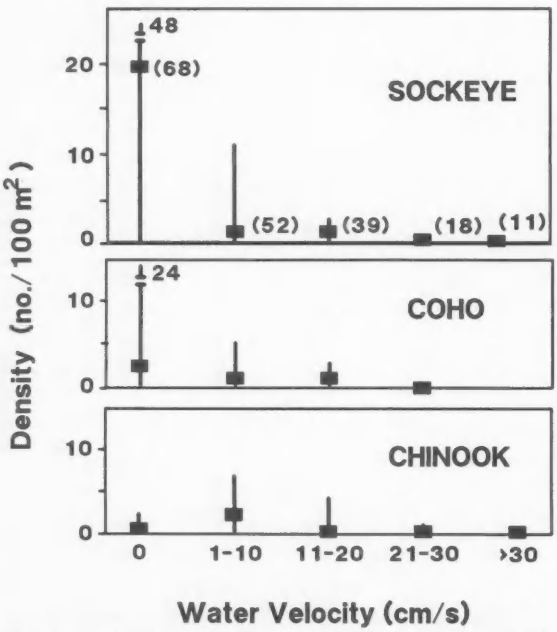

FIG. 6. Density of juvenile sockeye, coho, and chinook salmon in relation to water velocity at 188 seining stations in the lower Taku River, Alaska, July–September 1986. Symbols are medians, bars are interquartile ranges, and number of stations (*N*) is in parentheses.

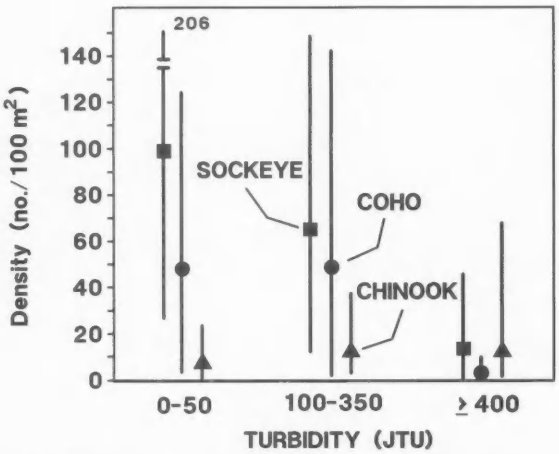

FIG. 7. Density of juvenile sockeye, coho, and chinook salmon in relation to turbidity in the lower Taku River, Alaska, July–September 1986. Data are from sites with suitable mean water velocity, based on relationships in Fig. 6 (≤10 cm/s for sockeye and coho, and 1–20 cm/s for chinook). Symbols are means and bars are ranges. Number of sites per species were 9–10 at 0–50 NTU, 4–5 at 100–350 NTU, and 16–18 at ≥400 NTU.

off-channel areas provide rearing habitat for an estimated 1 million juvenile sockeye, coho, and chinook salmon. This may be an underestimate, however, because of our methods. Seining within accumulations of woody debris probably underestimated true fish densities. Also, the number of sites was insufficient to provide reliable estimates of mean density for all habitat types, and some important areas may have been missed. Although much of the area covered by the aerial photographs was checked on the ground, some areas had poor access and could not be verified. Further, density data for fish were not normally distributed, and parametric statistics may have given biased estimates of total populations and confidence intervals. Thus, these estimates should be considered only approximations of the actual total populations of juvenile salmon in the lower river.

Two types of juvenile sockeye probably were present in the lower river: "river-type" sockeye, which rear in rivers for 1 yr; and "sea-type" sockeye, which migrate to sea as underyearlings (Wood et al. 1987). Based on adult scales, about 40% of the adult sockeye that spawn in the mainstem Taku River went to sea as underyearlings, and 60% wintered in fresh water (McPherson and McGregor 1986). Age-0 sockeye migrate to sea from the Taku River primarily from late June through September at a mean FL of 55 mm (Murphy et al. 1988). Thus, many of the juvenile sockeye we caught in the river may have been migrating to sea and only temporarily rearing in the lower river. River-type and sea-type sockeye also are present in other

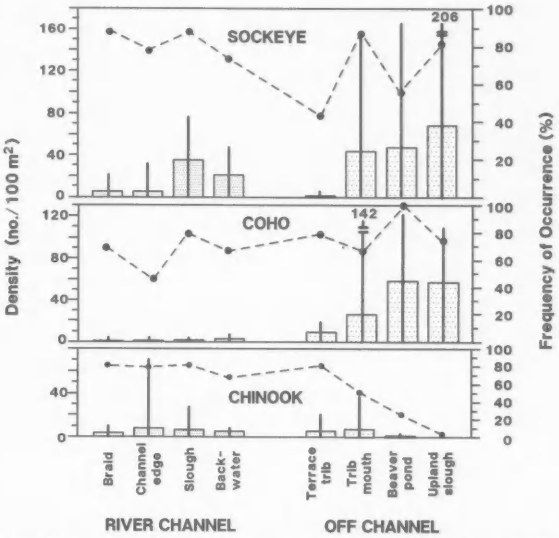

FIG. 8. Density and frequency of occurrence of juvenile sockeye, coho, and chinook salmon by habitat type in the lower Taku River, Alaska, July–September 1986. Histograms and bars show mean and range of density; shaded circles connected by dashed lines show frequency of occurrence. Number of sites sampled per habitat is shown in Table 2.

glacial Alaska rivers, including the Copper, Stikine, and Susitna Rivers, as well as smaller, nonglacial rivers of the northeastern coast of the Gulf of Alaska (McPherson 1987).

Densities of salmon in the lower Taku River were comparable to other studies. The range in mean density of coho in off-channel habitats (9–59 fish/100 m^2) was similar to the range in density in numerous small streams in Southeast Alaska (18–74 fish/100 m^2; Elliott and Hubartt 1983; Murphy et al. 1984; Murphy et al. 1986). In ponds and upland sloughs, mean sockeye density per unit water volume (0.38 fish/m^3; based on area seined and depth of the net or habitat) was within the range of densities in Babine Lake, B.C. (0.1–1.7 fish/m^3; Johnson 1961), and was greater than the average for Southeast Alaska lakes (0.1/m^3; J. Koenings, Alaska Department of Fish and Game, P.O. Box 3150, Soldotna, AK 99669 USA, pers. comm.). Mean chinook density in channel edges (8 fish/100 m^2) was similar to the density (14 fish/100 m^2) in channel edges of the Stikine River, Alaska (J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data) but less than 15% of chinook density in an Idaho stream (56–69 fish/100 m^2; Hillman et al. 1987).

Size and Growth

Changes in size of juvenile salmon indicate apparent growth. From early July to mid-September, mean FL of sockeye and chinook increased 0.25 and 0.15 mm/d, respectively, and the mean FL of both species in September (58 and 66 mm, respectively) was similar to the mean FL of age-1 smolts (65 and 76 mm, respectively) that migrate to sea in June (Murphy et al. 1988). Mean FL of age-0 coho increased 0.14 mm/d, but the mean FL attained in September (49 mm) was only 58% of the mean FL of age-1 smolts (85 mm) that migrate to sea in June (Murphy et al. 1988). Growth of age-0 coho probably was

TABLE 3. Area, mean fish density, and total population of juvenile salmon by habitat type in the U.S. part of the Taku River. Standard error of fish density is in parentheses.

Habitat type	Area (ha)	Area (%)	Fish density (No./100 m^2) Sockeye	Coho	Chinook	Total population (thousands) Sockeye	Coho	Chinook
River habitats								
Main channel*	1342	69.5	0	0	0	0	0	0
Braid	408	21.1	5.5 (4.1)	1.0 (0.8)	3.4 (1.6)	224	41	139
Channel edge	36	1.9	5.8 (2.2)	1.0 (0.3)	8.4 (4.4)	21	3	30
Slough	36	1.9	35.8 (12.7)	1.2 (0.4)	6.5 (5.1)	129	4	23
Backwater	9	0.5	21.1 (14.2)	2.9 (2.6)	5.1 (2.6)	19	3	5
Off-channel habitats								
Terrace tributary	52	2.7	1.4 (1.2)	9.4 (3.9)	5.3 (4.0)	7	49	28
Tributary mouth	29	1.5	44.2 (24.0)	26.3 (23.1)	7.5 (5.8)	128	76	22
Beaver pond	13	0.7	47.9 (39.7)	58.6 (27.6)	0.9 (0.9)	62	76	1
Upland slough	7	0.4	73.4 (45.6)	58.2 (26.9)	0.0 (0.0)	51	41	0
Totals	1932	100.2				641	293	248
95% Confidence interval						±451	±173	±184

*Main channels were too swift to seine, and were assumed not to contain rearing salmon because of swift current.

underestimated because of ongoing migration of newly emerged coho into the study area.

Except for beaver ponds, apparent growth was similar in the different habitat types. Mean FL of sockeye and coho were larger in beaver ponds than in other habitats, indicating faster growth because of higher temperature. The increasing trend in mean chinook FL from the U.S./Canada border toward the river mouth probably was not caused by differences in temperature, as temperature of the river did not differ longitudinally within the study area. Instead, the increase in chinook FL toward the river mouth may have been caused by different times of migration into the lower river from upstream. The larger fish closer to the river mouth may have emerged and migrated to the lower river before the smaller chinook upstream.

Habitat Utilization

Distributions of fish primarily depended on water velocity, and salmon used all types of habitat except where current exceeded 30 cm/s. In some streams (Lister and Genoe 1970; Everest and Chapman 1972), chinook and coho inhabit areas with current as fast as 70 cm/s where coarse substrate (20–40 cm diameter) provided cover from the fast current. In the active channel of the lower Taku River, substrate is mostly compacted gravel, sand, and mud, providing little cover from the turbulent flow, and the only suitable habitat occurs along the channel edge. In comparable streams with heavy sediment loads in New Zealand and Idaho, chinook also primarily used areas with current less than 30 cm/s (Glova and Duncan 1985; Hillman et al. 1987).

The river's turbidity had only a secondary influence on fish distribution, even though such high turbidity should severely impact fish. Bisson and Bilby (1982) showed that juvenile coho avoid turbidity greater than 70 nephelometric turbidity units (NTU), which is much lower than the typical 200 NTU of the Taku River in summer. Coho did avoid the river, perhaps because of turbidity, but sockeye and chinook occurred in both the turbid river and in clearwater off-channel areas. Lloyd et al. (1987) deduced that turbidity affects Alaska fishes by reducing aquatic primary production and impairing feeding. Being an optical property, turbidity is a poor measure of abrasive properties of suspended sediment (Warren 1971), and the glacial silt in the Taku River may not adversely affect fish. Turbidity effects, furthermore, were confounded with other differences between the river and off-channel habitats. For example, habitat stability, as measured by fluctuations in water level, was greater off channel than in the river.

Although the salmon species showed significant overlap, competition probably was important in only a few types of habitat. Competition between coho and chinook probably was unimportant because of low overlap in habitat, and because high turbidity and low fish density probably minimized social interactions in the river. As in the Sixes River, Oregon (Stein et al. 1972), coho and chinook occupied different habitats (coho in off-channel areas and chinook in the river), probably without actual territorial conflict. Competition between coho and sockeye, however, could occur because both species reached high density in upland sloughs and beaver ponds where clear water allowed visual contact. Differences in diet could alleviate such competition. In sloughs of the lower Fraser River, B.C., sockeye ate mostly Cladocera and Copepoda (Birtwell et al. 1987), which differs from the typical coho diet of Chironomidae, Plecoptera, and Ephemeroptera in streams (Koski and Kirchhofer 1984).

Suitable sites in the lower river frequently were unoccupied by juvenile salmon, apparently because of incomplete colonization. Spawning habitat is limited in the lower Taku River; most spawning in the mainstem is 15–50 km upstream of the U.S./Canada border; although tributaries along the lower river have some spawning populations (Eiler et al. 1988; Elliott and Kuntz 1988). Thus, many of the juvenile salmon in the lower river originated from upstream, and underuse of habitat probably resulted from incomplete colonization by downstream migrants. Even in lakes, for example, limited dispersal can cause inefficient use of rearing area. More than two-thirds of the juvenile sockeye in Babine and Nilkitkwa Lakes, B.C., concentrated in only 11% of the available rearing area near their entrance to the lakes (Johnson 1956).

Beaver dams present further obstacles to colonizing fish. Sockeye were present in only one-half of the beaver ponds. Coho were present in all the ponds but were mostly age-1 parr; age-0 coho were usually scarce or absent. The low frequency of occurrence of age-0 sockeye and coho indicates that the ponds were not fully colonized. Colonization of beaver ponds along the lower Taku River probably requires high water levels, such as during Tulsequah River floods (Thedinga et al. 1988) or fall freshets (Peterson 1982).

Salmon production possibly could be enhanced if the lower Taku River habitats were fully colonized by fish. Full colonization of off-channel habitat is needed to maximize smolt production because these areas provide most of the suitable rearing habitat for sockeye and coho. Although off-channel habitats comprise only 5% of the lower river's total area, they contained 39 and 83% of the total summer populations of juvenile sockeye and coho, respectively. Because salmon populations in glacial rivers have not been adequately studied, information is lacking on population dynamics and species interactions. Additional research, therefore, is needed to define factors that limit salmon production in the lower river before enhancement programs are initiated.

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Temporal and Spatial Dynamics of a Coastal Pelagic Species, *Sardinella maderensis* off the Ivory Coast

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Mendelssohn, R., and P. Cury. 1989. Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis* off the Ivory Coast. Can. J. Fish. Aquat. Sci. 46: 1686–1697.

Variations of fortnightly catch-per-unit-effort (CPUE) of *Sardinella maderensis* off the Ivory Coast is studied both in time and in space–time. Using multivariate time series models, lagged values of coastal sea surface temperature (SST) and salinity explain 33% of the variation of CPUE during this period. When optimal transformations are estimated, 55% of the variance is explained. The optimal transformations suggest that good catch rates are associated with local upwelling or oceanic frontal structures. However, the model differs significantly from previous models that examine the CPUE for the combined catches of the fleet. The model is shown to produce reasonable forecasts for the next two years. In space–time, evidence is presented that suggests that the migration of the fish between areas is related to movement of structures in the ocean. The relationships between CPUE and the environment are again highly nonlinear, so that linear analysis, such as correlation analysis, will be of limited use in examining these questions.

On étudie dans le temps ainsi que dans l'espace et le temps les variations des prises par unité d'effort (PPUE) de *Sardinella maderensis* observées à tous les quinze jours au large de la Côte d'Ivoire. Quand on utilise des modèles de séries chronologiques à plusieurs variables, les valeurs décalées de la TMS et de la salinité près des côtes expliquent 33 % de la variation des PPUE observée pendant cette période. L'estimation des transformations optimales permet d'expliquer 55 % de la variance. Ces transformations donnent à penser que de bons taux de capture sont associés à une remontée locale ou à des fronts océaniques. Cependant, le modèle diffère sensiblement des modèles précédents qui étudient les PPUE en fonction des prises regroupées de la flottille. On montre que le modèle fournit des prévisions raisonnables pour les deux prochaines années. Sur le plan spatio-temporel, on présente des faits qui portent à croire que la migration de ce poisson entre les secteurs est liée au déplacement de structures dans l'océan. Les relations fonctionnelles entre les PPUE et l'environnement sont une fois de plus fortement non linéaires, de sorte que l'analyse linéaire, comme l'analyse de corrélation, sera d'une utilité restreinte pour l'étude de ces questions.

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In a previous paper (Mendelssohn and Cury 1987) we studied the temporal dynamics of the combined pelagic species of the fishes off the Ivory Coast and how environmental processes affected the combined species dynamics, ignoring any spatial dynamics. There is reason to believe, however, that the dynamics of the combined species, which is of the greatest importance to the fleet, may differ from the dynamics of any individual species. If the biology of the individual species differs significantly, only broad oceanographic processes may appear to be affecting the dynamics, while different, more local processes may be affecting a particular species. Therefore, in this paper, we focus our attention on the dynamics of the catch rates of the dominant pelagic species caught in this area, *Sardinella maderensis*.

Determining the factors that affect changes in pelagic fish abundance, availability, and distribution, is complicated since the fish show a preference both for certain contemporaneous environmental conditions as well as for a particular history of the water masses and their food content (Mendelssohn and Roy 1986; Cury and Roy 1987; Mendelssohn and Cury 1987). A purely spatial analysis would blur these features, suggesting little relationship with the environment. Thus a dynamic, temporal approach is required.

The continental shelf off the Ivory Coast is affected by two upwelling seasons: a main season that occurs around June to September and a weaker, shorter season around January and February (Morlière 1970; Picaut 1983). Both sea surface temperature and salinity in this area vary seasonally and the intra-year variability in fish availability has been shown to be influenced by this variability (Marchal 1967). Marchal and Picaut (1977) present evidence that the strength of the local upwelling off the Ivory Coast, which is partly influenced by the configuration of the continental shelf, induces differential pelagic fish distributions. These fish distributions will fluctuate in space due to the dynamics of the water masses (Marchal 1967; ORSTOM/FRU 1976). Thus a temporal approach by itself also is not sufficient to explain the variability in fish availability — a spatial approach is required.

Understanding intra-year variations in indices such as catch-per-unit effort (CPUE) that reflect availability or abundance of a fish species is important to fisheries management. Studies have suggested that environmental conditions affect availability and hence fishing success (see for example Belvèze and Erzini 1983). During any given year there are probably several environmental factors that may influence fish availability, such as: sea temperature, salinity, dissolved oxygen, water mass boundaries, color and turbidity of the water, river outflows etc. (Bakun and Parrish 1980; Laevastu and Hayes 1981). Robust forecasts for fisheries need to be based on an understanding of the processes involved and should also help to clarify and increase our understanding of how the climatic factors influence the fish population.

Our interest in this paper is to determine the environmental processes that are important to the dynamics of *S. maderensis*, the form of these relationships, and to see to what extent spatial aggregation of fisheries data distorts these relationships. We analyze, using catch rate data, the changes in CPUE of this species through time, treating the entire area in aggregate, as well as the spatial–temporal dynamics of the species, that is the changes in time as well as the simultaneous changes in the distribution in space. As indicators of the environment we use sea surface temperature (SST), the sea temperature at 5 m depth (SST5M) and salinity at 5 m depth (SAL5M). These variables are chosen because they are the most complete and readily available environmental series and because they tend to reflect broad changes in the ocean environment.

Our models lead us to the conclusion that the dynamics of an individual species may differ considerably from that of an assemblage of related species. The interpretation of possible causal mechanisms affecting the population dynamics also differs when we examine the species in space and time, rather than in either dimension alone. We also examine the ability of the spatially aggregated model to provide forecasts of future catch rates.

Methods

As in our previous paper, our main methods of analysis are multivariate time series techniques. We fill in missing data using an algorithm of Shumway and Stoffer (1982). This algorithm fits to the data an autoregressive (AR) model (in this case of lag 2) of the form:

$$(1)\quad x(t) = Ax(t-1) + w(t)$$

$$(2)\quad y(t) = Hx(t) + v(t),$$

where $x(t)$ is a p-dimensional vector of the underlying population at time t, $y(t)$ is a q-dimensional vector of the observed data, H is a $q \times p$ known matrix, A is a $p \times p$ matrix of parameters to be estimated, $w(t)$ is an independent, identically distributed random vector distributed as normal $(0,Q)$ and v is an independent, identically distributed random vector distributed as normal $(0,R)$. The algorithm uses a variant of the EM algorithm (Dempster et al. 1977) to find maximum likelihood estimates of A, Q, and R as well as minimum mean square estimates of the $x(t)$. A rationale for using AR(2) models is given in Mendelssohn and Cury (1987).

To find local trend lines in the data we use the LOWESS scatterplot smoother (Cleveland 1979). This smoother is a two pass algorithm. In the first pass, each point is estimated using a weighted regression of all points within a given neighborhood of the point to be estimated. The second step corrects the estimate for outliers.

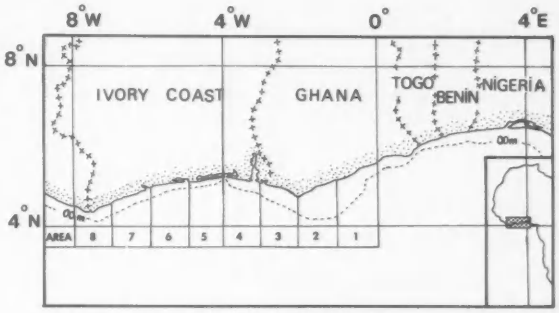

FIG. 1. Location of areas studied off the Ivory Coast.

Given data from a set of k time series, we consider a class of stochastic difference equations called vector autoregressive moving average models (or ARMA models for short) of the form (Tiao and Box 1981)

$$(3)\quad \Phi_p(B) z_t = \Theta_q(B) a_t,$$

where

$$(4)\quad \Phi_p(B) = I - \Phi_1 B - \ldots - \Phi_p B^p,$$

$$(5)\quad \Theta_q(B) = I - \Theta_1 B - \ldots - \Theta_q B^q$$

are matrix polynomials in B, the Φ's and Θ's are $k \times k$ matrices, $z_t = Z_t - \eta$ is the vector of deviations from some origin η that is the mean if the series is stationary, and $\{a_t\}$ with $a_t = (a_{1t}, \ldots, a_{kt})$ is a sequence of random shock vectors, identically, independently and normally distributed with zero mean and covariance matrix Σ. We follow the identification and estimation scheme described in Tiao and Box (1981) and Tiao et al. (1980), also used in our previous paper (Mendelssohn and Cury 1987).

We emphasize that throughout the paper we fit true multivariate models, not transfer-function or so called ARMAX models. There are some technical differences between the two models, which are most important when we are looking at space–time dynamics and are modeling both CPUE and the environment. Vector ARMA models, since they include the interaction between all the variables, tend to better take into account the intercorrelations between various different environmental series. These points are discussed further in Tiao and Box (1981, p. 804) and in Tiao et al. (1980).

At points in the paper we also use a subset autoregression procedure developed by Akaike (Akaike et al. 1979) to help identify the appropriate model form for estimation. This is a complicated procedure based on the Householder transformation and the AIC information measure and the reader is referred to the reference for a complete description of it.

Most techniques such as regression fit a linear, additive model to the data of the form

$$(6)\quad y(t) = u + \sum_{i=1}^{N} \beta_i x_i(t) + e(t).$$

A simple, natural extension is to fit additive models of the form

$$(7)\quad T(y(t)) = a + \sum_{i=1}^{N} s_i(x_i(t)) + h(t),$$

where $T(\,)$ and the $s_i(\,)$ are possible nonlinear transformations

TABLE 1. Values of the coefficients of the multivariate AR(2) model used to estimate missing values in the CPUE time series.

	Area 4 CPUE		Area 5 CPUE		Area 6 CPUE		Area 7 CPUE	
Area	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$
4	0.03	0.04	−0.05	0.04	−0.19	0.43	0.29	0.29
5	−0.05	0.02	0.03	0.02	0.02	0.27	0.05	0.13
6	0.04	0.02	0.02	0.13	0.36	0.22	0.04	−0.01
7	0.08	0.08	0.10	−0.19	−0.22	0.51	0.26	0.42

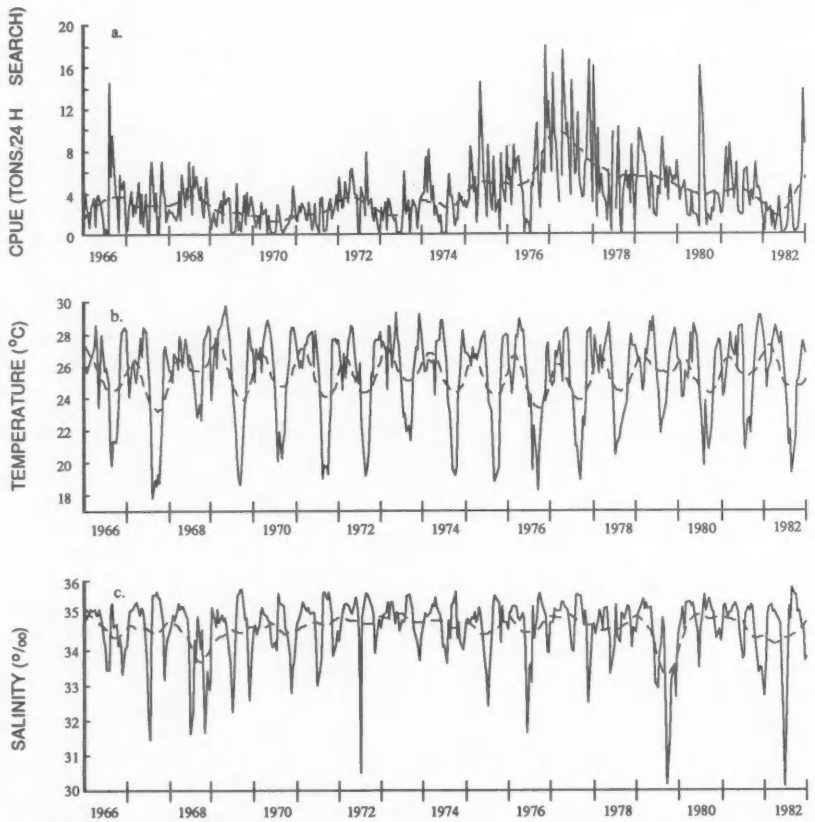

FIG. 2. Time series and estimated local trend for (a) aggregate CPUE, (b) SST, and (c) salinity.

of the data. In most problems, the form of these functions is not known a priori. The ACE (Alternating Conditional Expectations) algorithm of Breiman and Friedman (1985) empirically estimates the transformations that will have the smallest normalized residual error. In the bivariate case, this is equivalent to finding the transformations that produce the highest correlation. As the method is empirical, the form of each transformation is found by plotting the transformed data versus the original data. In the fisheries literature this algorithm has been used successfully by Mendelssohn and Cury (1987) and Mendelssohn and Mendo (1987).

Data

Biological Data

The pelagic fishery off the Ivory Coast has been described previously (Marchal 1967; FAO 1974, 1982), and Fonteneau and Marchal (1970) describe the data collection and data summarization procedures. *Sardinella maderensis* is the primary species exploited by the purse seiners based in Abidjan. The average annual landings of *S. maderensis* are about 10 000 t (mean for 1966–82); this is approximately 50% of the total Ivoirian catch of small pelagic species.

For purposes of our analysis, the Gulf of Guinea off the Ivory Coast was divided into eight areas each one degree in longitude and extending from 4°N of latitude to the coastline (Fig. 1). Measures of effort based on the time the boats spent searching for fish have been calculated using the method described in Fonteneau and Marchal (1970). CPUE for areas 4 to 7 was calculated for each fortnight from 1966 to 1982. (Fortnights in this context are periods of one-half month, not of 2 wk. Therefore each "fortnight" can vary in duration by up to several

TABLE 2. Parameters estimate and SE of the model using SST5M and SAL5M time series.

	Period 1966–1982		
Lag	Parameters	Estimate	SE
1	LNCPUE	0.304	0.049
	SST5M	−0.057	0.025
	SAL5M	0.028	0.012
2	LNCPUE	0.144	0.048
	SST5M		
	SAL5M		
4	LNCPUE		
	SST5M		
	SAL5M	−0.098	0.042
5	LNCPUE		
	SST5M	−0.078	0.026
	SAL5M	0.120	0.053
6	LNCPUE	0.192	0.046
	SST5M		
	SAL5M	0.073	
13	LNCPUE		
	SST5M	−0.062	0.014
	SAL5M		

days). Areas 4 to 7 are those where most of the catch of *S. maderensis* was taken. CPUE for each area was calculated by dividing the total catch in that area by the total search time for the boats in that area for the entire fortnight.

Mendelssohn and Cury (1987) discuss this measure of CPUE and possible problems that can arise when using it as a measure of local abundance. These problems are further compounded in this instance because it is not clear how to partition the measure of effort to reflect the effort expended only for *S. maderensis*. Using total effort as we do in this paper is not a completely satisfying alternative, because the fishermen fish for many species and for many periods, so the level of effort may be independent of the abundance of *S. maderensis* due to the presence of other species in the area.

The CPUE time series has missing data points, because an absence of fishing effort does not necessarily imply an absence of fish. Each of the areas 4–7 has about 10% of the data missing. The estimated parameters of the AR(2) model given in equations (1) and (2), used to fill in the data (Table 1), suggest a west to east migration and possible return. For example, CPUE in area 4 is significantly influenced by CPUE in areas 6 and 7 both 1 and 2 fortnight earlier (the last four values of the first row of the table) while area 7 is influenced by the past history of areas 6 and 7 and to some extent that of area 5 (the last row of the table).

Use of the completed data series in forming the space–time model will introduce more bias than in Mendelssohn and Cury (1987), due to some circularity in the process. The missing values of CPUE are estimated by an AR(2) model based on CPUE in all the areas during the surrounding time periods. Thus estimates of inter-area migrations might be affected by the filled-in data. Also, as only one species is being investigated, there are many more periods where there was effort but no catch of this particular species. This increases the likelihood that the form of the relationships is nonlinear, and that simple linear tools such as correlation studies or regression-like models will not be adequate. However, as only 10% of the data are missing, the filled-in data would have to have high leverage to greatly affect the final parameter estimates. As a further assurance that

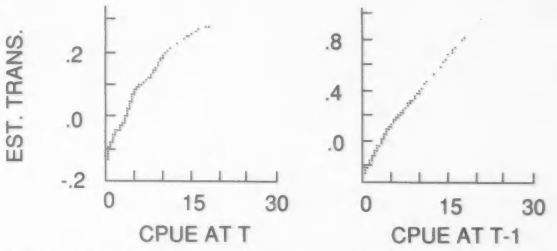

FIG. 3. Estimated optimal transformations of CPUE for predicting spatially aggregated CPUE.

the filled-in values have not unduly influenced our results, we checked the stability of our parameter estimates to the inclusion or deletion of data and compared our results for consistency with independent observations on the fishery.

The AR(2) model estimated by the missing data algorithm produces smoothed estimates of the data, including observation error. The smoothed values in each area (not shown) are close to the observed values when both exist and are consistent with other areas when one area has data and the second area does not. The completed time series of CPUE for each area were formed by substituting the smoothed estimate for each missing data point (see below).

A time series of CPUE aggregated across areas was calculated as the catch for all areas divided by the total effort (Fig. 2a). The localized trend, calculated using the LOWESS scatterplot smoother (Cleveland 1979), shows a slight dip in 1970, a slight rise and then a dip in 1972–73, and then a steady rise in CPUE to 1977. From mid-1977 onward, the trend has been downward until the start of an upturn in 1982.

Environmental Data

The environmental series consisted of SST data collected by merchant ships in the areas and SST5M and SAL5M collected by the Centre de Recherche Océanographique of Abidjan at a coastal station near Abidjan. Mean values were calculated for each fortnight to coincide with the fisheries data and missing data were filled in as in Mendelssohn and Cury (1987). SST aggregated across areas was calculated as the mean of the SST data by area.

The SST5M time series (Fig. 2b) shows a slight cooling trend until the end of 1967 followed by a slight warming trend until mid 1969. Since then there is no long-term trend in the data. The years 1969, 1973, 1978, and 1979 had noticeably warmer temperature minimums, while 1967 had a colder temperature minimum.

The SAL5M time series (Fig. 2c) also shows little long-term trend, except for sharp drops in 1968 and 1979. The years 1972, 1979, and 1982 also had significantly lower salinity minima.

Temporal Models of Aggregate Data

In this section we examine spatially aggregated CPUE for *S. maderensis* (actually we use LNCPUE = ln(CPUE + 0.5)) and the environment. The approach of this section closely parallels Mendelssohn and Cury (1987) so that we can illuminate the differences between the dynamics of the dominant, more coastal *S. maderensis* from the dynamics of the combined species, many of which are more oceanic.

Identification

Sardinella maderensis is a more coastal species than some of the other pelagic species, and SST averaged over such a wide area is not a very accurate reflection of the conditions faced by a stock which only is fished near the coast. Seemingly then, the coastal station data should better reflect the environmental conditions that affect the fish. However, the coastal station data were taken near a river estuary and thus also may have not reflected the actual temperatures that the fish experienced. For these reasons, two different models were examined: one using LNCPUE, SAL5M and average SST, and one using LNCPUE, SAL5M and SST5M.

We model the dynamics by identifying and estimating a vector ARMA model of the form (2). We simultaneously model LNCPUE and the environmental variables. This is especially important for our data as SST and salinity tend to be highly intercorrelated. To identify the proper form of the model (AR, MA, or ARMA) and the appropriate lags to be included in the model, we examined the cross-correlation matrices and the generalized partial-correlations (Tiao and Box 1981). The autocorrelation functions of SST and SST5M showed a strong annual seasonal cycle, while that of SAL5M showed a 6-mo cycle with perhaps a smaller annual seasonal term. The autocorrelation function of LNCPUE did not suggest a seasonal cycle; there were significant peaks around lags of 1, 6, and 12 fortnights.

The cross-correlation functions between LNCPUE with SST or SST5M showed persistent significant correlations at lags of roughly five to 15 fortnights. The partial-correlations were significant at only a few lags both for LNCPUE with itself and with the environmental series. The decaying behavior of the cross-correlations coupled with the spikes in the partial-correlations suggested that an AR model was appropriate (Tiao and Box 1981).

The lags suggested by the partial-correlations were then used in an exact maximum likelihood routine (Tiao et al. 1980) to estimate the AR parameters. Nonsignificant parameters were then removed from the models, and any additional parameters suggested by the residual covariance matrices were added to the models. In general, the model using SST5M tended to give both a better overall fit to the data as well as better behaved residual series. For this reason, we will concentrate on this model only. The estimated parameters to model LNCPUE are (see Table 2 for the complete model):

$$\begin{aligned}\text{LNCPUE}(t) = {} & 0.304*\text{LNCPUE}(t-1) + 0.144*\text{LNCPUE}(t-2) \\ & + 0.191*\text{LNCPUE}(t-6) - 0.057*\text{SST5 M}(2t-1) \\ & - 0.078*\text{SST5M}(t-5) \; - 0.062*\text{SST5M}(t-13) \\ & + 0.028*\text{SAL5M}(t-1) \; - 0.098*\text{SAL5M}(t-4) \\ & + \; 0.120*\text{SAL5M}(t-5) \; - 0.073*\text{SAL5M}(t-6).\end{aligned}$$

The residual cross-correlation matrices showed no lack of fit for this model, and the normalized residuals appeared to satisfy most of the Gaussian assumptions of the model. The model using SST5M explained 33% of the variance in LNCPUE. The model does a particularly good job at predicting the large peaks in LNCPUE.

Improving the Model Predictions

There are a priori reasons to believe that the relationships between CPUE and the environment are nonlinear or discontinuous in nature. For example, there is most likely a maximum temperature beyond which the fish are not found in abundance; a further increase in the temperature will not change the number of fish. Likewise, there probably is a minimum temperature below which the fish are not found; a further decrease in temperature will have no additional effect. Marchal (1967) notes that outside the optimum ranges for temperature or salinity the relationships may be very different in form than within the optimum ranges.

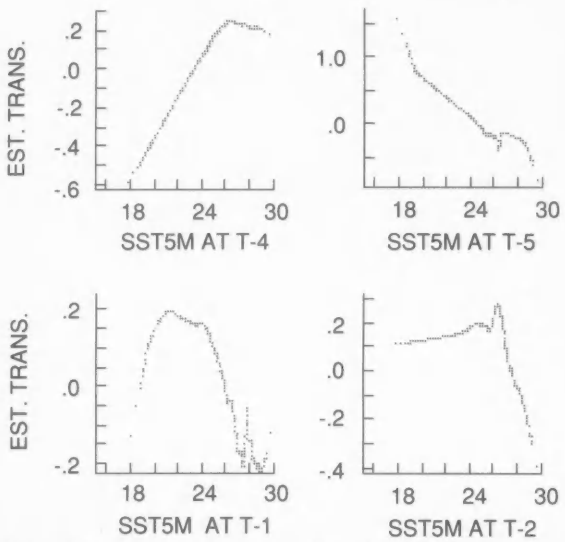

FIG. 4. Estimated optimal transformations of SST5M for predicting spatially aggregated CPUE.

The models we have estimated so far are all linear. To obtain a more realistic model, we used a technique due to Breiman and Friedman (1985) that calculates optimal transformations for a given dependent variable and a set of predictor variables, while preserving an additive structure to the model.

It is necessary to reidentify the proper model (i.e. what variables and what lags to use as predictors) for the transformed case, as it is possible that if the optimal transformations were known a priori, then variables that were not important predictors on a linear scale might become important predictors on the transformed scale. To this end, predictor variables to be included in the final model were selected by a stepwise procedure. First, all lag one variables were included in the model, entered in order of CPUE, SST5M, and SAL5M. (Some studies have shown that the order of the variables affects the transformations. We always enter CPUE first, so that any bias is conservative for environmental effects.) Any variable that was essentially transformed into a constant was removed.

Then models with lags 1 and 2, lags 1,2,3, etc. were used in the transformation algorithm, up to a lag of 15 fortnights. If the addition of the three variables in a new lag did not decrease the residual variance to a significant degree, then the entire lag was not included in the model. This stepwise procedure is highly nonoptimal and may well select a set of variables whose transformations do not explain as much variance as some other set of variables. Surprisingly, we ended up with a model very similar to the linear model in terms of the variables included in the model. However, the form and interpretation of the model differed substantially from the linear AR model.

The transformed model explained 55% of the variance of the transformed CPUE, a substantial increase over our original

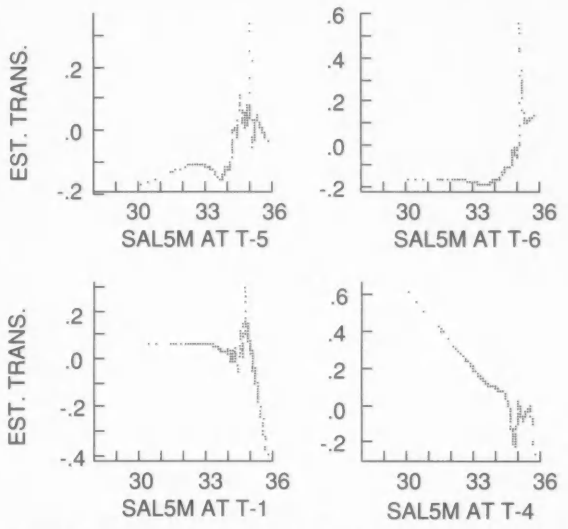

FIG. 5. Estimated optimal transformations of SAL5M for predicting spatially aggregated CPUE.

model. The transformations for CPUE at time t and at a lag of one fortnight are both very close to the natural log transformation selected a priori in our original models (Fig. 3). The estimated transformation for SST5M displays behavior consistent with our a priori reasoning (Fig. 4).

There is an increase in value between 18 and 20°C, a nearly constant value to 24°C, a sharp drop to 27.5°C, and a small rise to 28°C before dropping again. This suggests that at one period previous, conditions are most favorable between 20 and 24°C, dropping off sharply if the water is either colder or warmer. The small rise around 28°C may be water that is at the boundary of a frontal structure (Bakun 1978).

The estimated transformation for SST5M two fortnights earlier (Fig. 4) suggests that there is a slight preference for temperatures between 27–28°C, but mainly that temperatures greater than 28°C are not desirable. At four fortnights previous, the transformation of SST5M is linear with an asymptote around 26°C, while at five fortnights earlier the transformation is nearly linear with a preference for colder waters.

The transformation of SAL5M at one fortnight earlier (Fig. 5) suggests a preference for salinity at 35‰, with a strong avoidance of any greater density. The period from six to four fortnights prior shows a preference for a density in a narrow band centered at 35‰ at both six and five fortnights earlier, followed by a transition to relatively low densities of salinity. If this occurs at the same time that colder water is being replaced by warmer water, then CPUE should be particularly high.

Forecasting

The parameters for the linear model using LNCPUE, SST5M, and SAL5M were reestimated using data only from the years 1966–80. The new parameter estimates were close to the old ones, with no significant difference in the form of the estimated model. These parameter estimates were then used to calculate one-step ahead forecasts of CPUE, i.e., forecasts that assumed that at the start of each fortnight the data from the last fortnight were available. This would be equivalent to a real-time forecasting system.

The forecasts were transformed back to the original scale using the unbiased inverse transform (Granger and Newbold 1977):

$$(8)\quad \mathrm{CPUE}(t) = \mathrm{EXP}(\mathrm{LNCPUE}(t) + 0.5*(\mathrm{SE}**2)),$$

where SE is the standard error of the forecast on the transformed scale. The forecasted values for 1981 and 1982 (Fig. 6) describe quite well the increase of CPUE during the main upwelling season which began in fortnight 13 in 1981 and fortnight 14 in 1982. The model does not forecast as well during other parts of the year.

Implications of the Analysis

It is not surprising that our linear model explains only 33% of the variance in CPUE of *S. maderensis* and predicts only broad changes in CPUE. This is a multispecies fishery that is not targeted on any one species. There does not appear to be a good way to partition effort between the species, and thus our measure of CPUE is highly biased and may only roughly reflect availability or abundance of *S. maderensis*. A single species that is more coastal in its distribution is more likely to have different environmental features dominate its dynamics during different times of the year. That is, the problem is nonstationary while we have restricted ourselves to stationary models.

Nevertheless, our model has a biological interpretation that is consistent with previous studies, and the differences between this model and our previous model for all species combined (Mendelssohn and Cury 1987) reflect known differences between *S. maderensis* and most of the other species. Moreover, the improvement in fit when transformations were calculated suggests that much of the relationship with the environment is nonlinear and only roughly approximated by a linear model.

Mendelssohn (1990) examines the affects of the optimal transformations in the frequency domain, both for the combined species model and for the models of *S. maderensis* only. For the combined species, LNCPUE, as compared with CPUE, shifts the spectral peak from a period of approximately 1 mo to a peak centered at a period of 5 wk. The estimated transformations for SST5M and SAL5M also shift the spectral peaks to the same frequency band, thus aligning the spectral peaks in all three series.

Both transformed SST5M and transformed SAL5M are strongly coherent with LNCPUE for the combined species at this frequency band, but partial coherences (the frequency domain equivalent to partial correlations) show that only transformed SST5M is important. The coherence between LNCPUE with transformed SAL5M is due to the coherence between transformed SST5M and transformed SAL5M.

For *S. maderensis* only, Mendelssohn (1990) shows that while the coherences between LNCPUE for *S. maderensis* with transformed SST5M and transformed SAL5M are significant at the same frequency bands, the partial coherences are significant at different time scales. Transformed SST5M shows significant partial coherences at lower frequencies, while transformed SAL5M has significant partial coherences at higher frequencies.

Our analysis of CPUE for all species combined revealed no relationship with salinity (Mendelssohn and Cury 1987). Our present models, particularly after the transformations, indicate that salinity is a crucial variable in predicting the CPUE of *S. maderensis*. In addition, a coastal measure of SST5M provided a better fit than a more offshore measure of SST. This is con-

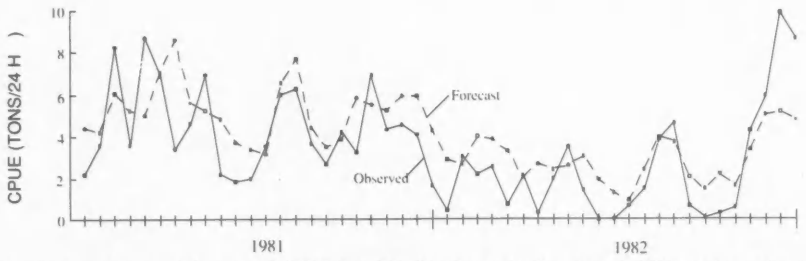

FIG. 6. One-step ahead forecast of CPUE for 1981–82 when only data through 1980 used to estimate the model.

sistent with the known fact that *S. maderensis* is a highly coastal species that is sensitive to salinity (FAO 1974). CPUE is predicted by CPUE lagged one, two, and six fortnights. The lags of one and two fortnights suggest that CPUE for *S. maderensis* is persistent. The lag at six fortnights may reflect environmental conditions occuring at that lag. Picaut (1983) shows that SST in the area has a spectral peak around a frequency of 45 d. The environment side of our model also suggests important behavior at this lag.

The lags of SST5M and SAL5M in the model, while open to interpretation, are not as immediately obvious. The model says that higher levels of CPUE will be found when starting six fortnights earlier, the waters make a transition from cooler, high-salinity waters to warmer, low salinity waters. This interpretation is strengthened by the estimated transformations, which show quite sharply the transitions from one type of water to another around four fortnights previous if CPUE is to be high. Why should a transition in the waters so much before the period of fishing affect CPUE so much? One possible answer is that at the beginning of the rainy season sudden and strong storms occur which decrease the salinity of the water. Upwelling usually starts about four fortnights later. The river outflows during this period bring terrigenous materials to the sea, and through a series of links, this improves the zooplankton productivity in the area (Binet 1976, 1983), the food of that species (Dia 1972). We emphasize that while this explanation has events occurring in the proper sequence, so might other explanations. Our model does not validate this explanation.

While a number of assumptions have been made, it appears that the enrichment in the food, which is triggered by environmental changes, plays an important role in the observed fluctuations in CPUE for *S. maderensis*. While the fish may be sensitive to salinity levels, salinity and temperature variables appear to reflect more a dynamic process that creates the proper conditions for the fish, rather than absolute measures of the conditions that are favorable to the fish. That the dynamics of the dominant species, *S. maderensis*, differs to a great extent from the dynamics of the combined species suggests that it may be preferable to aggregate forecasts of individual species rather than to forecast the aggregate behavior.

Space–Time Models

The general pattern of the seasonal migration for *S. aurita* off the Ivory Coast and Ghana has been described in ORSTOM/FRU (1976), and Binet (1983) has analysed the similarities between the migratory pattern of *S. aurita* and the spatial dynamics of zooplankton in the same area. For *S. madernesis*, Marchal (1967) briefly speculates on possible migratory patterns between the areas, but otherwise not much is known of the migratory behavior of *S. maderensis*. Since environmental factors play an important role in the migrations of *S. aurita* we expect that the same may be true for the migrations of *S. maderensis* off the Ivory Coast. In this section we analyze the fluctuations in the CPUE and environmental time series across areas to clarify the patterns of migration and their possible linkages with climatic factors.

The spatially disaggregated CPUE series (Fig. 7) were modeled with area specific SST as the environmental series (Fig. 8), making a simultaneous model with eight series in total. The results of the previous section suggest that a more coastal measure of temperature would be preferable, as well as an area specific measure of the salinity of the water. However, these series were only available from the one coastal station.

For an initial analysis of the data we used a subset autoregression procedure due to Akaike et al. (1979) with a maximum allowable lag of 12 fortnights to construct a simultaneous model of the eight series. (Hereafter, SST4 will denote SST in area 4, CPUE4 will denote CPUE in area 4 etc.) The results of the subset autoregression (Table 3) were mixed. While the parameters for the model did seem to indicate a migratory pattern (discussed below) the fit to the data is quite low with an r-squared no better than .15 in any of the areas.

Due to the lack of fit in the space–time model, optimal transformations were calculated to predict the CPUE in each area using the same stepwise selection process as in the previous section. The variables were always entered lower order lags before higher order lags and CPUE series before SST series.

The transformations greatly increased the predictability of the transformed CPUEs, with r-squared values of .47, .50, .58, and .53 for areas 4,5,6, and 7, respectively. For each area, lags of one, two, and four fortnights were found to be important in predicting CPUE for that area. The migratory pattern suggested by the transformed series qualitatively was the same as suggested by the linear AR model. We will discuss the suggested migratory pattern and then examine the transformations in areas 4 and 7 more closely.

Migration

The transformed variables suggest that migration between areas is associated with higher or lower levels of CPUE in given areas during the preceding periods as well as the relative temperature of the water in each area and its movement between areas during the preceding time periods.

The overall pattern suggested by the transformed model (Figs. 9 and 10) is that areas 6 and 7 vary together, area 4 varies separately from the other areas, and area 5 is a transition zone. A major fishing area is located in area 7 but often overlaps into

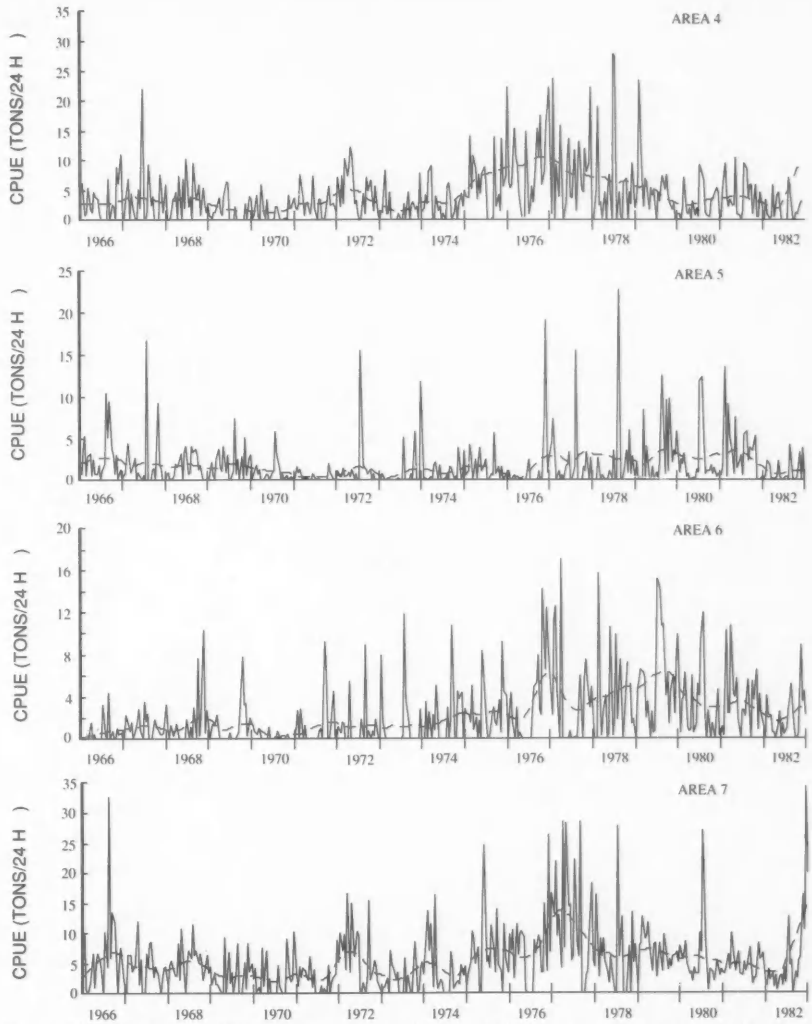

FIG. 7. Filled-in series of CPUE for *S. maderensis* by area. Solid lines are the data series while dashed lines are estimated local trend lines.

area 6. This probably explains why these two areas vary together.

In more detail, from the figures an east–west migration clearly appears in CPUE as shown in the one and two fortnight lags between areas 4 and 7. A reverse movement in CPUE is shown in the lags of one and four fortnights with area 4, indicated by the eastward pointing arrows in the figure.

A very similar pattern is seen for transformed SST (Fig. 10). An east–west migration, particularly from area 4 to areas 6 and 7 is seen, and at the same lags as with CPUE. A similar return migration is also seen, though the relationship with area 6 is not as clear as with CPUE.

The transformed SST suggests that CPUE4 is usually higher when area 6 and area 7 have environmental conditions that are associated with lower values of CPUE6 and CPUE7. Combining these observations, we suggest that the proposed migratory pattern may be due to the fish moving to the areas with the most favorable environmental conditions. The transformed SST (discussed below) appear to associate favorable conditions with frontal structure. The west-to-east movement probably reflects advection due to the Guinea Current while the east-to-west movement, reflects changes in upwelling (Bakum 1978; Picaut 1983).

Optimal Transformations

The main fishing areas are located in areas 4 and 7. Therefore we will only examine in detail the transformations for these two areas. The estimated transformation for CPUE7 (not shown) is very close to the log transformation that we have used throughout this paper for a priori reasons. The transformation of CPUE7 at time $t-1$ (not shown), however, suggests two regimes: a value of CPUE7 of 5 t per 24 h search or less and a value of CPUE7 of 10 t per 24 h search and greater. Generally, when CPUE7 has been high it tends to persist for two fortnights or longer at the high level. CPUE7 is generally higher when CPUE4 and CPUE6 were higher the previous fortnight. The

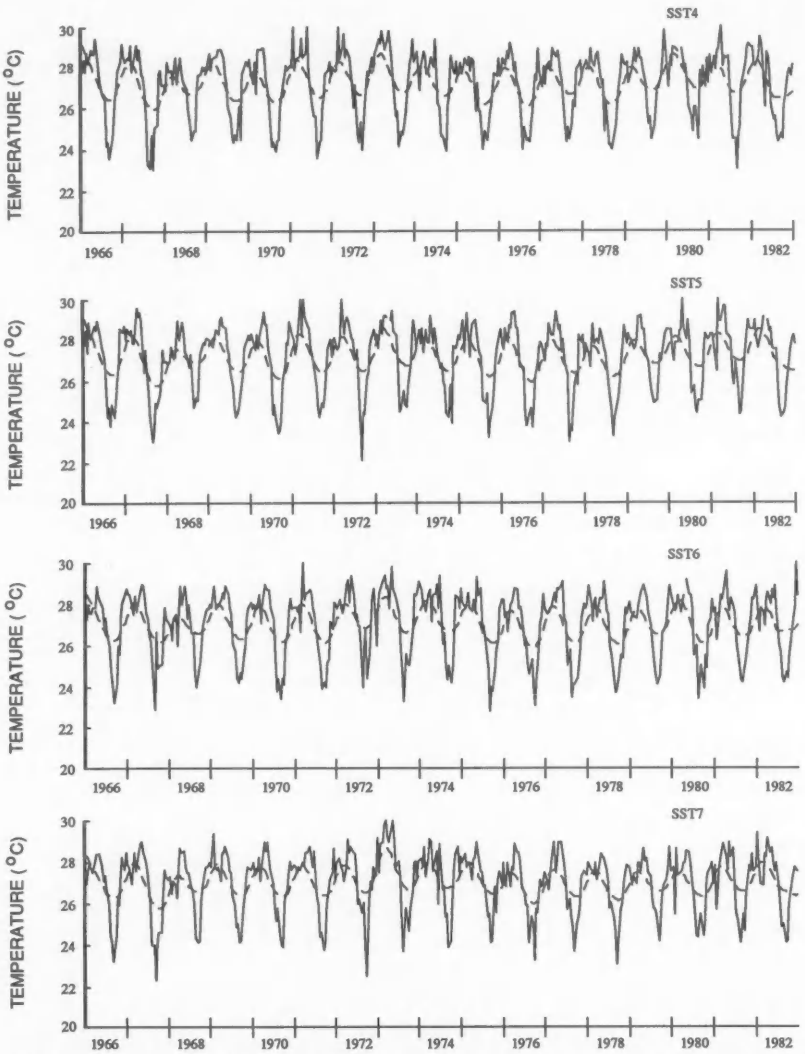

FIG. 8. Filled-in series of SST by area. Solid lines are the data series while dashed lines are estimated local trend lines.

transformations of CPUE at higher lags are similar in form, though they may be the inverse function.

The transformation of SST7 (Fig. 11) suggests three regimes: when the temperature is less than 24°C, when the temperature is between 24 and 28°C, and when the temperature is greater than 28°C. These values correspond with the isotherms used by Bakun (1978) to define the different oceanographic regimes in the area. Generally, CPUE7 is higher when SST7 two fortnights ago is less than 24°C, while SST7 one fortnight ago is greater than 25°C, preferably greater than 28°C. This suggests that the best fishing will occur in this area when there has been a transition in the water probably due to the passing through of a frontal structure.

A similar but not identical change in SST4 (Fig. 12) also leads to higher levels of CPUE7, though higher levels of CPUE4 occur when SST7 undergoes a change that causes lower levels of CPUE7. The transformed values of SST4 and SST7 one fortnight previous define to a large degree when there will be high levels of CPUE7 (greater than 10 t per 24 h search). If we plot SST4 one fortnight previous versus SST7 one fortnight previous and mark the points with high CPUE7 (not shown) the points with high CPUE7 show about the same distribution as the rest of the points. However, the same plot for the transformed variables (Fig. 13) shows that the points with a high CPUE7 are clustered in one region, to a large degree separated from the rest of the data.

The estimated transformations for area 4 (Figs. 14 and 15) have a similar interpretation. The transformation of the dependent variable CPUE4 (not shown) is also very close to a log transformation. Higher levels of CPUE4 will occur when SST4 makes a transition from colder waters two fortnights previous to warmer waters one fortnight previous (Fig. 14). At the same time SST7 should make a transition from warmer (but not too warm) to colder waters (Fig. 15).

TABLE 3. Model estimated by subset autoregression procedure due to Akaike for space–time model.

	Lag	LNCPUE4	LNCPUE5	LNCPUE6	LNCPUE7	SST4	SST5	SST6	SST7
1	LNCPUE4	.115			.137				
	LNCPUE5	−.041	.109		.015				−.182
	LNCPUE6	.006	.023	.212	.021			−.151	.064
	LNCPUE7	.017	.020	.042	.226			.128	−0.13
2	LNCPUE4	.089		.132	.157				
	LNCPUE5	−.087	.212	.123			.135		
	LNCPUE6	−.007	.045	.140			.029		
	LNCPUE7	.003	.039	.070			.025	−.123	
3	LNCPUE4	.099							
	LNCPUE5	.011							
	LNCPUE6	.016		.103					
	LNCPUE7	.023		.021					
4	LNCPUE4								
	LNCPUE5								
	LNCPUE6				.086				
	LNCPUE7				.017				
Initial variance		1.177	.866	1.106	1.111				
Residual variance		1.051	.752	.881	.900				

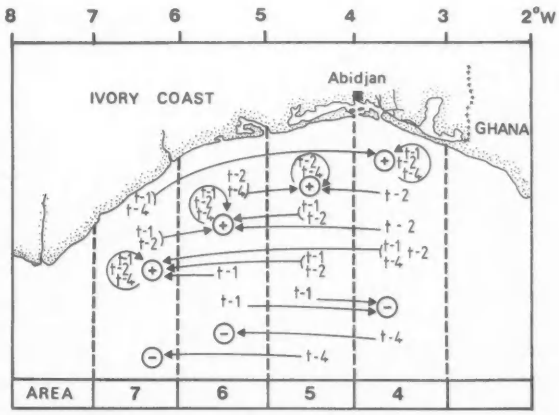

FIG. 9. Schematic representation of migration pattern in CPUE suggested by the transformed model. The plus or minus signs indicate the direction of the influence (higher or lower CPUE), the arrows show which areas affect other areas, and the time lags of the relationships are also shown.

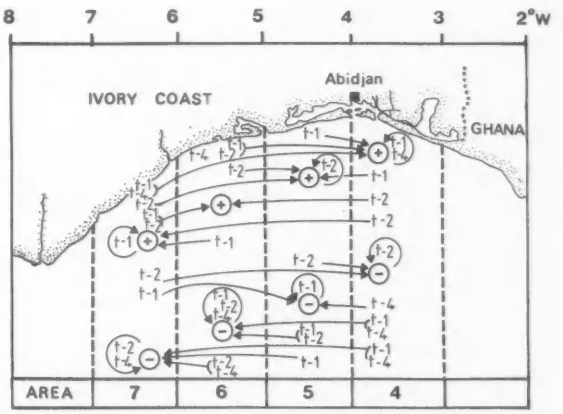

FIG. 10. Schematic representation of the propagation in SST suggested by the transformed model. The figure is interpreted as in Fig. 9.

Plots of transformed SST4 and SST7 through time (not shown) show that the ideal conditions in area 7 for high CPUE4 rarely occur at the same time as the ideal conditions in area 4. Thus CPUE4 tends to be higher either when conditions are favorable in area 4 but not too favorable in area 7 or when conditions are not unfavorable in area 4 but conditions in area 7 are very unfavorable. Unlike in area 7, SST4 and SST7 one fortnight previous are not sufficient to identify periods with high CPUE4. This suggests that the process in area 4 is more complicated, involving both what the fish are doing and more complicated behavior in the ocean.

Discussion and Conclusions

While there must be caution in making interpretations of our space–time analysis for reasons mentioned previously, the general pattern that emerges is that of a west-to-east migration followed by an east-to-west migration. The fish appear to migrate mainly between areas 7 and 4, perhaps avoiding the fishery in the central area by going too deep for the gear. Environmental processes, measured here by the dynamics in SST, appear to influence these migrations. Zooplankton are one of the major food sources for *S. maderensis*, and comparing this proposed migratory pattern with the dynamics of zooplankton in the same region provides a plausible rationale for the migration. During the main cold season there is a general enrichment of zooplankton with an eastern movement associated with the Guinea Current. The zooplankton then make a return migration to the west (area 7) around August, associated with an undercurrent (Binet 1976). During the warm season, the western part of the Ivoirian Gulf (area 7) is the area most favorable for zooplankton enrichment and fishing also usually is favorable during this period. Area 5 generally is the area poorest in zooplankton (Binet 1976) and also generally has the lowest levels in CPUE.

Fishermen in the area have observed a lack of fish in the central areas and an apparent rapid migration of fish from one area to another. It is difficult to compare two different biological processes, especially when the evidence is circumstantial, but there appears to be enough evidence to develop some ten-

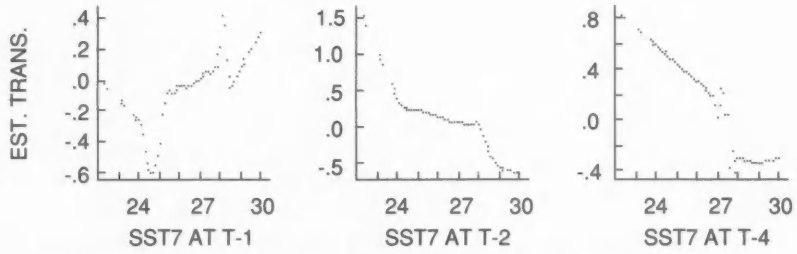

FIG. 11. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 7.

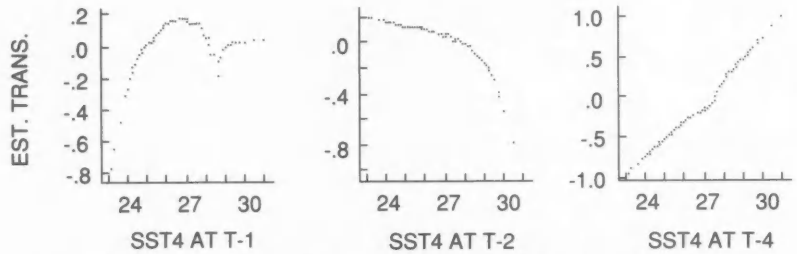

FIG. 12. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 7.

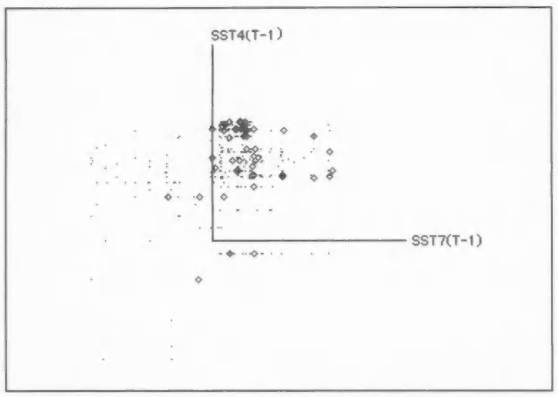

FIG. 13. Transformed SST7 versus transformed SST4. Diamonds mark time periods when CPUE in area 7 was high.

tative hypotheses and to point to the underlying environmental processes and fish behaviour that would have to be studied further to validate these hypotheses. The short (fortnight) time scales in which we find movement in the CPUE as well as the changes in the environment that lead to high levels of CPUE all seem to support the idea that the fish are migrating between areas where they can take advantage of sudden increases in zooplankton biomass caused by favorable environmental conditions (see Binet 1976). Further simultaneous studies of both zooplankton and *S. maderensis* in the same area would help to clarify some of these issues.

Our analysis has presented evidence that the dynamics of *S. maderensis*, both in space and time, appear to be influenced to a considerable degree by the environment. The space–time analysis suggests that the environment may be an indirect influence: favorable environmental conditions may be causing an increase in both the total biomass of the zooplankton as well as in the degree of aggregation of the zooplankton, as suggested by Binet (1976, 1983), and the fish move and take advantage of the increased biomass.

We have also shown that the relationships between CPUE and the environment most likely are highly nonlinear. If we are to better understand the dynamics, we must be careful to work on the appropriate functional scales. Simple linear methods will often obscure relationships that exist both in the data and in the real world. And finally, we have shown that the dynamics of an individual species, in this instance *S. maderensis*, can differ from the dynamics of the combined species of a fishery of which it is a part, both in terms of the behavior of the fish and in terms

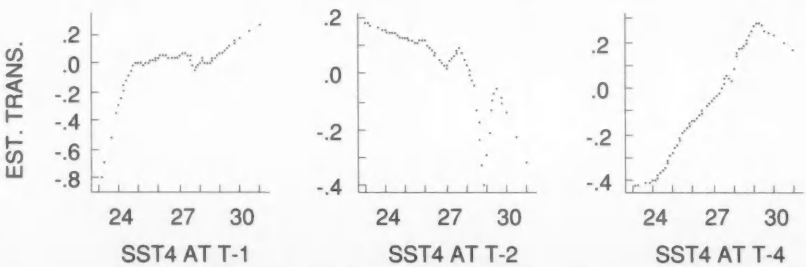

FIG. 14. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 4.

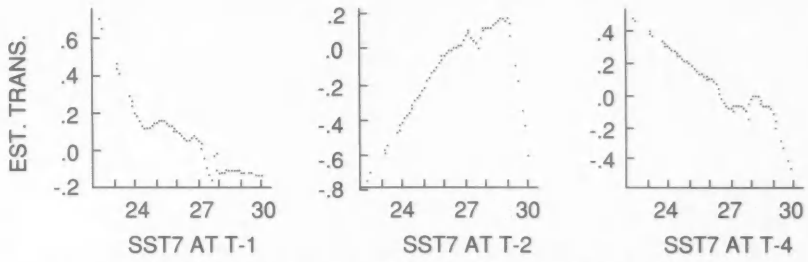

FIG. 15. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 4.

of the oceanographic processes that influence the fish. Management based on the combined species dynamics could lead to unforseen changes in the dominant species. An open, but important question, is whether management plans or forecasts based on an aggregate of models for individual species would outperform models of the aggregate dynamics.

Acknowledgment

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Effects of Snail Grazing on the Diversity and Structure of a Periphyton Community in a Eutrophic Pond

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Swamikannu, X., and K. D. Hoagland. 1989. Effects of snail grazing on the diversity and structure of a periphyton community in a eutrophic pond. Can. J. Fish. Aquat. Sci. 46: 1698–1704.

Periphyton diversity was highest at low to intermediate levels of grazing by the freshwater snail *Physella* and suppressed at high grazer densities, in partial support of the intermediate disturbance hypothesis. For the first time, the response curve of algal biomass versus a range of snail densities was used to establish low, intermediate, and high levels of community disturbance. *Physella* densities corresponding to these levels were added to net enclosures in a small eutrophic pond, to examine differences in attached algal cell densities and diversity after 20 d. Algal standing crop was enhanced in low and depressed in intermediate and higher grazer treatments. Five categories of attached algal response to grazing were identified: (1) filamentous algae suppressed at high grazing pressure; (2) rosette or filamentous taxa suppressed at moderate to high levels of grazing; (3) algae resistant to grazing via sediment-associated recruitment; (4) low profile algae with highest densities at moderate grazing, and; (5) prostrately attached taxa enhanced at moderate and high grazing levels. In contrast to marine macroalgal communities, the primary mechanism mediating community response to different levels of grazing was the morphology of algal attachment.

On a constaté que la diversité du périphyton était maximale lorsqu'il était peu ou moyennement brouté par l'escargot d'eau douce *Physella* et qu'elle devenait nulle lorsque le périphyton était davantage brouté, ce qui corrobore partiellement l'hypothèse de la perturbation moyenne. C'est la première fois qu'on se sert d'une courbe mettant en relation la réponse de la biomasse algale en fonction de la densité d'une population d'escargots pour définir la perturbation de la communauté végétale à un degré faible, moyen et élevé. En déposant des *Physella* dans des enclos aménagés au moyen de filets dans un petit étang eutrophe, on a créé des populations de densité correspondant à ces degrés de perturbation, afin de voir, au bout de 20 jours, les différences de densité et de diversité chez des algues fixées. La biomasse algale a augmenté lorsqu'elle était faiblement broutée et baissé lorsqu'elle était moyennement et fortement broutée. On a défini cinq catégories de réponses : (1) disparition des algues filamenteuses en conditions de broutage élevé; (2) disparition des algues en rosettes ou filamenteuses en conditions de broutage moyen ou élevé; (3) résistance au broutage par un processus de recrutement sédimentaire; (4) algues d'importance secondaire dont la densité est maximale en conditions de broutage modéré; (5) algues fixées à plat dont la densité augmente en conditions de boutage modéré et élevé. On a constaté que, contrairement à ce qui s'observe dans les communautés macro-algales marines, la morphologie de l'attache algale est le principal mécanisme par lequel la communauté a réagi au broutage.

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The intermediate disturbance hypothesis states that diversity is higher when disturbances are intermediate on the scales of frequency and intensity (Connell 1978). This hypothesis has often been invoked to account for high species diversity in natural habitats such as marine subtidal and intertidal zones (Lieberman et al. 1984; Sousa 1985) and stream benthos (Ward and Stanford 1983), as well as coral reefs (Connell 1979; Huston 1985). Grazing is an important factor that maintains high levels of diversity in both marine environments (Dayton 1975; Lubchenco 1978; Hay 1981) and freshwater phytoplankton communities (e.g. Porter 1977; Carpenter and Kitchell 1984; Carpenter et al. 1987).

A variety of freshwater grazers on periphyton have been studied, including: fish (Cooper 1973; Power and Matthews 1983; Stewart 1987), tadpoles (Dickman 1968), crayfish (Flint and Goldman 1975), stream insects (e.g. Eichenberger and Schlatter 1978; Lamberti and Resh 1983; Vaughn 1986; Steinman et al. 1987; Lamberti et al. 1987a), amphipods (Hargrave 1970), oligochaetes (Bowker et al. 1983; Kairesalo and Koskimies 1987), and particularly snails (e.g. Hunter 1980; Kesler 1981; Sumner and McIntire 1982; Mulholland et al. 1983; Cuker 1983b; Lodge 1986; Lowe and Hunter 1988). In addition, the impact of multispecies grazer assemblages on the periphyton has been examined by Cattaneo (1983); Cattaneo and Kalff (1986); and Lamberti et al. (1987b). Many of these studies have focused on the impact of specific grazers on community standing crop and productivity, especially in lotic systems. In general, moderate grazing pressure appears to reduce algal standing crops yet increase productivity in streams (Elwood and Nelson 1972; Gregory 1983) and lakes (Flint and Goldman 1975). It remains unclear, however, how grazing affects attached algal

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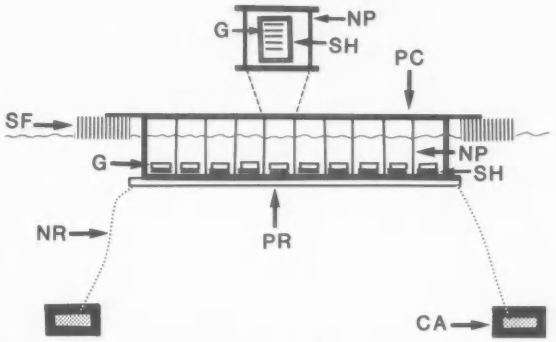

FIG. 1. Profile of sampler assembly (not drawn to scale). Inset is detailed top view of one compartment. SF = styrofoam float; G = glass slide; NR = nylon rope; NP = net partition; SH = slide holder; PC = PVC cage; PR = plexiglass rack; CA = concrete anchor.

diversity in both lotic and lentic systems across a wide range of grazer densities.

The purpose of the present study was to determine to what extent the intensity of grazing by the freshwater snail *Physella (=Physa) virgata* Gould affects attached algal diversity and density. Our approach was first, to determine the range of periphyton community response to a broad range of snail densities. The intermediate disturbance hypothesis was then tested by comparing periphyton diversity exposed to low, intermediate, and high snail densities.

Methods

The study was conducted in a 0.2-ha eutrophic pond at the Fort Worth Botanic Garden (Fort Worth, Tarrant County, Texas). Aquatic vascular plants near shore were densely populated by snails, primarily *Physella virgata*. Total alkalinity during the study period ranged from 99.2–109.7 $mg \cdot L^{-1}$ as $CaCO_3$, mean pH was 7.8, and water temperature ranged from 21–24°C.

Experimental Design

Three sampling cages (118.3 cm long × 28 cm wide × 17.8 cm deep) were constructed using 1.3-cm diameter polyvinyl chloride (PVC) pipe and 600-μm mesh netting (Fig. 1). A pair of styrofoam blocks was attached to each sampler to maintain submerged artificial substrates at a depth of 6 cm and the upper edge of the cages above the water surface to restrict snail immigration and emigration. Cages were partitioned with netting (600-μm mesh) into 10 compartments, each containing a slide box (9.5 × 8.5 cm) with five glass microscope slides (7.5 × 5 cm) positioned vertically. The sampler assembly was held in place in the pond by nylon ropes attached to two concrete anchors. Each compartment generated four samples, which accounted for within-sampler variability. Cages positioned at three locations in the pond served as replicates of the treatment series.

Preliminary Experiment

The sampling frequency and snail densities for low, intermediate, and high levels of disturbance were determined in a preliminary study conducted from March 14–April 18, 1985. Snails were collected near the site where the sampling cages were to be located. A cage partitioned into seven compartments was stocked with seven densities (4.2, 8.4, 16.8, 25.4, 33.6, 42.2, and 84.5 $snails \cdot m^{-2}$, based on the total netting, slidebox, and slide substrate surface area for each compartment) of *Physella*, 10 d after the cage was placed in the pond. Slides were collected at 10 and 25 d after snail introduction. The attached algal biomass was determined by measuring the percent transmission of light through the algal growth layer, according to Hoagland (1983). The sampling frequency for the main study was determined based on the rate of algal accumulation on the glass substrates. Levels of disturbance were chosen based on the relative decrease in attached algal biomass with increasing snail density observed in the preliminary study on day 35 (Fig. 2). To approximate the three major portions of this response curve (including a small increment in snail density to compensate for greater algal accumulation expected in late spring), snail densities in the main study were set at 12, 30, and 70 $\cdot m^{-2}$ to represent low, intermediate, and high levels of disturbance, respectively.

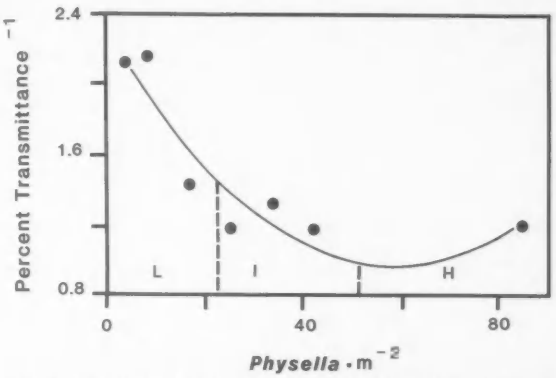

FIG. 2. Reciprocal of percent transmittance of light through growth layer (proportional to algal biomass) versus snail density, 25 d after snail introduction. Low (L), intermediate (I), and high (H) were snail densities chosen to represent the three disturbance levels. The best fit using step up regression was given by a second degree polynomial with the equation, $y = 2.3172 - 0.04619x + 0.000395x^2$. The last coefficient was significant at $P = 0.02$ in improving the prediction of y. Low, intermediate, and high regions were delimited by integrating for the area under the curve and determining the upper limits for one-third and two-thirds of the area. Low/intermediate and intermediate/high boundaries were at 23 and 52 $Physella \cdot m^{-2}$, respectively.

Main Study

Physella collected from the study pond were maintained in laboratory aquaria prior to use, with natural pond substrates as their principal food source. All snails used in the main study were of similar size (shell length approximately 5–7 mm) (because they developed from egg masses collected at the same time). On April 30, 1985, three sampling cages were placed 1 m apart in the pond, 1.5 m from the water's edge. After 7 d, snails were blotted, weighed, and added to the cages at 12, 30, and 70 $\cdot m^{-2}$. One slide was collected from each compartment to enumerate and identify the initial algal community. The 10 compartments in each cage were treated as follows: one pair was allocated to each of the three disturbance levels, two served as controls (no snails) and two had the netting removed, exposing them to ambient grazing in the pond. Both the assignment of compartment treatments and the selection of compartments

to be sampled on each date were random. One slide box (four slides) was collected from each of the five treatments in each of the three cages, 10 and 20 d after snail introduction.

Grazers from the pond accessed uncaged substrates by floating to the water surface or crawling up the anchoring lines. These grazers included *Physella virgata, Heliosoma anceps, Lymnae stagnalis appressa*, chironomid larvae, amphipods, and unidentified aquatic insect larvae. Ambient snail densities (all species) on uncaged slides averaged $115 \cdot m^{-2}$ on day 27, with *Physella* accounting for 82%. Chironomid densities were $240 \cdot m^{-2}$ on uncaged slides and $10–33 \cdot m^{-2}$ on caged slides on day 7, whereas amphipods and aquatic insect larvae were observed in negligible numbers and not in all treatments.

The change in wet weight (mass) of snails in each compartment was determined at the time of sampling. Change in weight was chosen instead of *Physella* density or biomass as a measure of disturbance intensity, because it takes into account variation in individual snail grazing activity through time.

In the laboratory, each slide was scraped and apportioned into four subsamples: (1) one half of side A was scraped into a beaker, treated with concentrated HCl to remove all organic matter, and the residue brought up to a known volume. One millilitre was then allowed to dry on a (22 mm^2) coverslip and mounted in Hyrax for determination of diatom cell densities and taxonomic identifications; (2) one-third of side B was scraped into a known volume of buffered deionized water in plastic bags for immediate identification of nondiatom algae; (3) one-third of side B was treated with 5% glycerin in water for several days until 100% glycerin remained and then mounted in a drop of melted glycerin jelly to provide a semi-permanent slide for intact community observations; (4) the final third of side B was scraped into 10 mL of 2% glutaraldehyde in filtered pond water for nondiatom algal identifications and living versus nonliving diatom counts.

Diatom taxonomic identifications were made using an Olympus Model FH microscope with a 100× planachromat objective (numerical aperture = 1.3). Five hundred valves were counted in strips on permanent slides and diatom cell densities were calculated. A plot of the number of taxa encountered versus 20 intervals of 25 valves each, for both an early sample and a highly grazed late sample gave asymptotic curves, indicating that 500 valve counts were adequate to include the majority of taxa present in each community. Diatom cell densities on the glass slides did not influence the number of taxa encountered ($r = -0.19$). Nondiatom algae were enumerated with a Palmer cell at 400×, by counting 30 random Whipple fields.

Nonliving diatom counts (based on the absence of protoplasmic material) were performed by preparing a wet mount and counting 100 cells at 100×. Taxa that constituted more than 10% in the permanent slide counts were tallied individually whereas the remaining taxa were grouped into a single category. Both a two-way ANOVA and Friedman's nonparametric test on living versus nonliving diatom cell percentages ($\bar{x} = 10\%$), using one sample per compartment, indicated no significant differences between replicates or between treatments. A similar analysis on cell percentages of living versus nonliving *Achnanthes minutissima* Kütz., the dominant diatom in all samples on day 27, gave identical results. Consequently, further analyses of living versus nonliving diatoms were not performed.

Data Analysis

Diversity (H') was calculated using the Shannon–Wiener Index (Shannon and Weaver 1949), where 6.2 would indicate maximum diversity and 0.0 the minimum (given 500 valve counts). Community comparisons were made using Stander's similarity index (SIMI) (McIntire and Moore 1977). This index ranges from zero for communities with no taxa in common, to one for communities which are identical. Species richness comparisons were done using a standard two-tailed t-test and diversity comparisons were made using a modified t-test (Zar 1984, p. 146), with pooled replicates.

Statistical analyses of treatment effects were based on the model of the two-way ANOVA with repeated measures on one factor (Winer 1971). This ANOVA accounts for the autocorrelation of samples through time, that is, the lack of complete independence of time-series samples. A posteriori testing to determine which of the treatments were significantly different was done with the Student-Newman-Keuls test. Correlation, single- and two-factor ANOVA's, and polynomial regressions were done using the MINITAB statistical package (Penn. State Univ., 1981, Version 1.0).

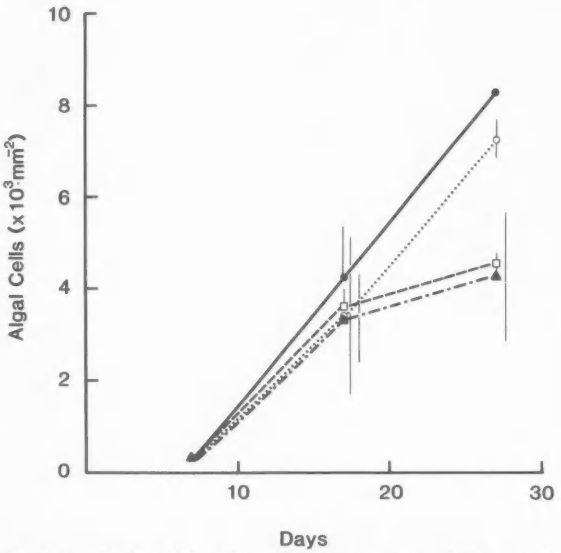

FIG. 3. Attached algal densities under four treatment regimes over the 27-d study period. (○) = control; (●) = low; (□) = intermediate; (▲) = high. $n = 3$; $\bar{x} \pm$ SD.

Results

Attached algal cell densities increased significantly in all treatments throughout the study ($P = 0.003$; $F = 23.59$; Fig. 3). Differences in snail densities had a significant effect on algal densities 20 d after snail introduction ($P = 0.004$; $F = 10.52$), with the highest algal cell densities (8.3×10^3 cells$\cdot m^{-2}$) occurring at the lowest grazing intensity (Fig. 4A). Algal cell densities in the control and low snail density treatments were significantly higher than those in intermediate and high density treatments ($P < 0.05$).

Algal diversity and taxa richness were highest at low to intermediate snail densities 20 d after snail introduction (Fig. 4B and C); suppression of algal diversity and taxa richness, as compared with controls, was apparent only at high grazer densities. Although the high and intermediate grazer treatments were not significantly different in algal cell density ($P > 0.05$; Fig. 3) or

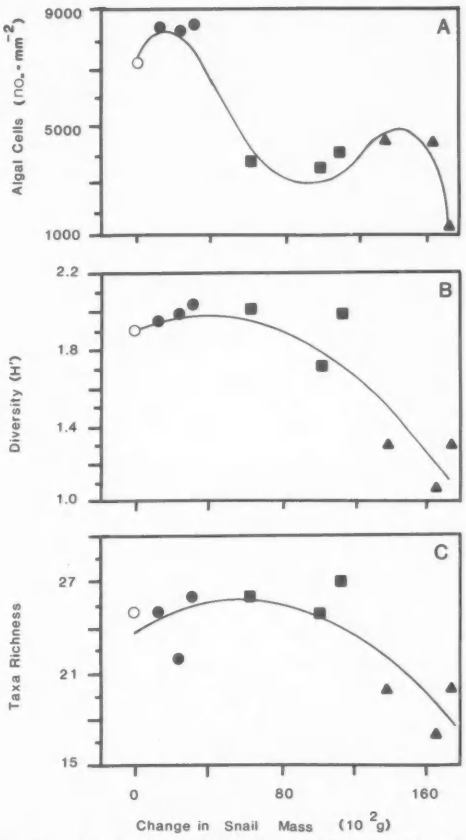

FIG. 4. (○) = control, (●) = low, (□) = intermediate, and (▲) = high. (A) Attached algal cell density 20 d after snail introduction versus change in snail mass, a measure of disturbance intensity. The single value for control is a mean of two replicates, one having been excluded because of snail immigration. The best fit using step up regression was given by a fourth degree polynomial with the regression equation, $y = 7280.5 + 161.7x - 6.221x^2 + 0.060\,54x^3 - 0.00017793x^4$. The last coefficient was significant at $P = 0.01$ in improving the prediction of y. No biological significance is attributed to the small peak at high snail densities. (B) Diversity (H') as a function of change in snail mass. The single value for the control is the mean of two replicates. Although H' is ordinal, the mean was chosen since calculation of a median was not possible. The best fit using step up regression was given by a second degree polynomial with the regression equation, $y = 1.9206 + 0.004234x - 0.00005101x^2$. The last coefficient was significant at $P = 0.05$ in improving the prediction of y. (C) Functional relationship between taxa richness and grazing intensity. The single value for control is the mean of two replicates. The best fit using step up regression was given by a second degree polynomial with the equation, $y = 23.719 + 0.07332x - 0.000616x^2$. The last coefficient was significant at $P = 0.05$ in improving the prediction of y.

community similarity (SIMI = 0.99; Table 1), there was a significant difference in their diversity ($P < 0.005$) and taxa richness ($P < 0.001$; Fig. 4).

Comparisons of uncaged compartments and controls (no snails) indicated that nine of the 12 dominant taxa were significantly different in the two treatments ($P < 0.05$; Fig. 5); three were lower in the uncaged versus control compartments and six were higher. Uncaged substrate cell densities [$6.9 (\pm 2.3) \times 10^3$ cells·mm^{-2}] were similar to controls on day 27, whereas algal diversity and species numbers in uncaged compartments were higher ($H' = 2.4$; $S = 31$).

TABLE 1. SIMI values for comparison of attached algal communities from different treatments.

Treatments			SIMI
Control	versus	Low	0.99
Control	versus	Intermediate	0.97
Control	versus	High	0.93
Low	versus	Intermediate	0.96
Low	versus	High	0.92
Intermediate	versus	High	0.99
Uncaged	versus	Control	0.92
Uncaged	versus	Low	0.91
Uncaged	versus	Intermediate	0.98
Uncaged	versus	High	0.98

A total of 142 diatom and 12 nondiatom taxa were identified and enumerated. Nondiatom algae accounted for less than 0.5% of the total algal cell density in any treatment 20 d after snail introduction. Taxonomic responses to grazing intensity were inferred from 12 diatom taxa, each having constituted at least 10% of the total algal cell density in any one sample (Fig. 5). Five distinct categories were evident based on the pattern of response:

(1) *Melosira varians* was suppressed at high levels of grazing.
(2) *Fragilaria capucina* var. *mesolepta*, *F. vaucheriae*, *Nitzschia palea*, and *Synedra rumpens* var. *familiaris* were suppressed at moderate and high grazing.
(3) *Achnanthes minutissima* and *Nitzschia amphibia* were insensitive to grazing.
(4) *Achnanthes lanceolata* var. *omissa*, *A. exigua* var. *heterovalva*, and *Amphora perpusilla* attained maximum densities with intermediate grazing. Although not significant in the caged treatments ($P > 0.05$), their densities in the uncaged treatment were significantly higher than in the control.
(5) *Cocconeis placentula* var. *euglypta* and *C. placentula* var. *lineata* increased in density at intermediate and high grazing levels.

Discussion

The enhancement of algal cell densities at low *Physella* grazing levels is consistent with the results of other marine and freshwater studies (e.g. Flint and Goldman 1975; Carpenter 1981; Lamberti and Resh 1983), and was likely a result of an increase in algal cell turnover generated by the removal of senescent cells (Cuker 1983a; Jacoby 1985). Although indirect factors such as nutrient regeneration can significantly affect periphyton responses to grazing (Flint and Goldman 1975; Kairesalo and Koskimes 1987), such factors may be insignificant in most natural attached algal communities (Cuker 1983b). Direct comparison of the results of the present study with many previous experiments is difficult, because grazer impact studies have typically employed natural snail densities as the "intermediate" level of grazing, without determining community response to a range of grazer densities. Natural snail densities range widely between habitats, for example 7.7–23 (Cuker 1983b), 45–107 (Kesler 1981), and 450·m^{-2} (Jacoby 1985), thus confounding between-study comparisons.

In this study, algal density was suppressed at intermediate and high grazing, and diversity was higher at low to interme-

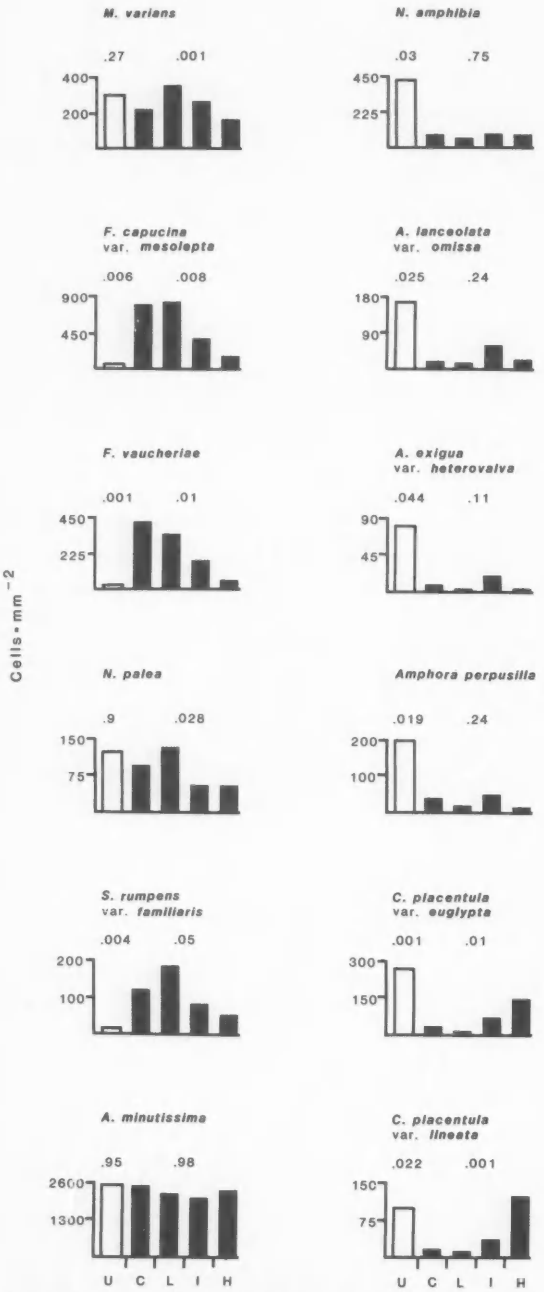

FIG. 5. Response of dominant diatom taxa to snail grazing intensity. Probabilities from the repeated measures ANOVA are given above each histogram, on the left for the effect of caging (uncaged versus control) and right for the effect of snail grazing. Cell densities are mean values for the two sampling dates. U = uncaged (ambient grazing), C = control (no snails), L = low, I = intermediate and H = high grazer density.

diate levels of grazing, in partial support of the intermediate disturbance hypothesis. Marine macroalgal studies indicate that this hypothesis will hold only when the dominant alga is preferred by the principal grazer (Lubchenco 1978; Lubchenco and Gaines 1981). Similar diversity responses have been suggested for marine (Hunter and Russell-Hunter 1983) and freshwater (Atlas 1984) microalgal communities, however the dominant alga in this study, *Achnanthes minutissima*, was unaffected by increased grazing (Fig. 5). A similar lack of response by *A. minutissima* to increased grazing was observed by Lowe and Hunter (1988).

The assertion that the presence of a dominant resistant to grazing should cause no appreciable change in diversity (Lubchenco 1978) may explain the similarity in diversity between periphyton communities exposed to low and intermediate grazing in the present study. At high levels of grazing, the significant decline in diversity resulted from the elimination of subdominant taxa (Peet 1974; cf. Fig. 4B and C). Projections from marine studies may not have predicted such a dramatic decline in diversity because macroalgal communities are considerably less diverse than diatom-dominanted, freshwater assemblages. This diversity-dependent response may also explain why previous laboratory studies employing freshwater microcosms with limited species pools failed to detect a change in diversity with high levels of grazing (see Kehde and Wilhm 1972).

The resistance of some freshwater diatoms to grazing is probably a combined result involving several factors. While firmness of adhesion and nature of attachment is important for resistance to grazing (Kesler 1981; Sumner and McIntire 1982; Hudon 1983; Pringle 1985), the present study indicates that recruitment dynamics can be an overriding factor. The dominant alga in this study was resistant to grazing; *A. minutissima* was observed primarily attached to sand grains that settled on the glass slides, rather than being directly attached to the glass surface (based on observations of intact communities from glycerin mounts). This observation strongly suggests that the dominance and apparent resistence of *A. minutissima* in this community were more likely related to sand-facilitated recruitment. Suspended sand grains and silt are known to be important vehicles of transport for diatom colonizers (Pringle 1985; Rosowski et al. 1986b). Further, recruitment of diatoms from the water column can be of greater importance in substrate colonization than direct encroachment by motile diatoms from the surrounding community (Hoagland et al. 1986).

Differences in species composition between uncaged and control compartments indicated that water movement, consequent algal immigration, and perhaps grazing by other herbivores such as chironomids were additional factors structuring the natural pond periphyton. Uncaged substrata exhibited the highest algal diversities observed despite the highest grazing pressure, again indicating that immigration was most important. Enclosure effects on water-borne recruitment have been observed in other diatom community studies (Peterson 1986).

While the response of marine macroalgal taxa to grazing may be dependent on the food preferences of the dominant grazer (Lubchenco 1978), the vulnerability of attached microalgae seems to be highly dependent upon their morphology (Lowe and Hunter 1988). A filamentous morphology, for example, facilitates ingestion by herbivores (Nicotri 1977; Hunter 1980; Hudon and Legendre 1987). In this study, the filamentous diatom *M. varians* declined temporally in all treatments in proportion to the intensity of grazing, and the filamentous taxa *F. vaucheriae* and *F. capucina* var. *mesolepta* were suppressed at intermediate to high levels of grazing (Fig. 5). Vertically oriented algae such as *S. rumpens* var. *familiaris* and *N. palea*, which form rosettes directed away from the substrate (Hustedt

1930; Hoagland et al. 1982), similarly declined at intermediate to high grazing pressure.

Two varieties of *Cocconeis placentula*, a prostrately attached diatom, were found in greatest abundance in the high grazer communities (Fig. 5). The enhancement of *Cocconeis* spp. at high grazing has been documented in both marine and freshwater studies (Patrick 1970; Hunter 1980; Kesler 1981; Nicotri 1977). Although there is no evidence for active avoidance of *Cocconeis* by snails (Higashi et al. 1981), diatoms with prostrately attached frustules are apparently difficult to dislodge mechanically (Hunter 1980; Kesler 1981). *Cocconeis* was also observed epiphytic on *Oedogonium*, where it was undoubtedly susceptible to snail grazing, thus illustrating the importance of the site as well as the morphology of attachment.

The three diatoms that reached maximum cell densities at moderate grazing (*Amphora perpusilla*, *Achnanthes exigua* var. *heterovalva*, and *A. lanceolata* var. *omissa*) are small taxa that may have responded to a reduction in vertically oriented diatoms. Competition for space is thought to occur in attached algal communities (Hoagland et al. 1982); at higher grazing pressure the relatively large *Cocconeis* possibly outcompetes these smaller taxa for space. *Achnanthes lanceolata*, a prostrate alga that binds to substrates by mucilage pads (Rosowski et al. 1986a), has also been previously reported to proliferate under moderate (Gregory 1983) and high grazing pressure (Steinman et al. 1987).

Although the diversity of attached marine macroalgal communities in response to grazing has been well studied (for overview, see Sebens 1985), the responses of freshwater attached algal communities are still not well understood. This study indicates that the intermediate disturbance hypothesis may hold true for freshwater attached algal communities with respect to the intensity of grazing disturbance, but that the mechanisms that result in high diversity at intermediate levels of grazing may be quite different in the two algal systems. Grazer food preferences may be less important in freshwater attached communities (Nicotri 1977; Lowe and Hunter 1988), rather the physical mechanics of snail grazing on surfaces predisposes the morphology of algal attachment as the major determinant of community composition.

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Molecular Divergence and Evolutionary Relationships in *Pontoporeia* (Crustacea: Amphipoda)

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Väinölä, R., and S-L. Varvio. 1989. Molecular divergence and evolutionary relationships in *Pontoporeia* (Crustacea: Amphipoda). Can. J. Fish. Aquat. Sci. 46: 1705–1713.

To evaluate hypotheses put forward to explain the origin of the "glacial relict" faunal element in North American and Eurasian lakes, the levels of genetic divergence among species and populations of the amphipod genus *Pontoporeia* were studied using enzyme electrophoresis. Genetic distances among the European fresh- and brackish-water *P. affinis*, the North American freshwater *P. hoyi*, and the marine *P. femorata* (from Europe) ranged $D = 1.5–2.8$, suggesting divergence times of the order tens of million years for all these lineages. An undescribed North American coastal species (*P. "affinis"*) was similarly distinct from *P. hoyi* and *P. femorata*, but more closely related to the European *P. affinis* ($D = 0.5$). No further systematic subdivision within these species was revealed in the examined material. The number of expressed isozyme loci was the same in *P. affinis* and *P. femorata* for all enzymes examined; the results provide no support for the hypothesis of a recent polyploidization event in the evolution of *P. affinis*, as earlier suspected on karyological grounds. All speculations on the role of the late Pleistocene glaciations in molding the currently recognized systematic structure of *Pontoporeia* were thus dismissed.

Afin d'évaluer certaines hypothèses avancées comme explication de l'origine de la relique faunique glaciaire dans les lacs nord-américains et eurasiens, on a étudié par électrophorèse enzymatique le degré de divergence génétique chez des espèces et des populations d'amphipodes du genre *Pontoporeia*. On a constaté que l'éloignement génétique (D) entre l'amphipode d'eau douce et d'eau saumâtre européen *P. affinis*, l'amphipode d'eau douce nord-américain *P. hoyi* et l'amphipode marin *P. femorata* (d'Europe) se situe entre 1,5 et 2,8, ce qui dénoterait des périodes de divergence de l'ordre de 10 millions d'années pour toutes ces lignées. On a observé la même différence entre, d'une part, une espèce côtière nord-américaine non décrite (*P. « affinis »*) et, d'autre part *P. hoyi* et *P. femorata*, mais *P. « affinis »* était plus proche du *P. affinis* européen ($D = 0,5$). L'examen des spécimens n'a révélé aucune autre subdivision systématique chez ces espèces. Pour toutes les enzymes étudiées, le nombre de loci d'isozyme exprimés était le même chez *P. affinis* et *P. femorata*; les résultats ne corroborent pas l'hypothèse de l'apparition récente de la polyploïdie dans l'évolution de *P. affinis*, comme on avait auparavant pensé après des études caryologiques. On a donc rejeté toutes les hypothèses avancées sur le rôle présumé des glaciations du Pléistocène supérieur dans le façonnement de la structure systématique actuellement reconnue chez *Pontoporeia*.

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The origin of the "glacial relict" element in the lake faunas of northern Eurasia and North America has puzzled zoogeographers for more than a century (e.g. Lovén 1862; Jägerskiöld 1912; Thienemann 1950; Ekman 1953; Segerstråle 1957, 1962; Ricker 1959; Holmquist 1966; Dadswell 1974). The element includes species of the crustacean genera *Mysis*, *Pontoporeia*, and *Limnocalanus*, as well as *Myoxocephalus* fish on both continents, and additional taxa peculiar to each region. The distribution of these species is largely confined to areas submerged by proglacial lake systems (or dilute seas) during the retreat of the last glaciation; they also inhabit the brackish Baltic Sea and many arctic estuaries, and a similar faunal element is present in the Caspian Sea.

It is now generally agreed that the "relicts" (also known as glacial immigrants, glacial opportunists, or the deepwater community) are descendants of refuge populations that survived along the southern margins of the continental ice caps over the last glacial maximum (e.g. Ricker 1959; Segerstråle 1962; Dadswell 1974). However, the degree of relationship of the freshwater species to their marine congeners, and the relationships between the freshwater populations of the two continents still remain disputed issues; the suggested time scales range from some tens of thousand to some tens of million years. The controversy has naturally also been reflected in the systematic treatment of the species involved. This also concerns the amphipod genus *Pontoporeia*, whose members play dominant roles in soft-bottom communities both in northern lacustrine and brackish-water environments.

The early hypotheses on the origin of the relict species maintained that the lacustrine populations of different areas had been derived from marine progenitors and had acquired their freshwater tolerance independently of each other, as they became isolated from their original coastal habitat through geological changes at the end of the glacial period (e.g. Lovén 1862; Thie-

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nemann 1950). Holmquist (1959, 1966) later strongly advanced an opposite view, that the relicts are actually old and stable freshwater species with a history of lacustrine life dating back to the mid-Tertiary (though they have also retained their euryhalinity). However, the idea of a Pleistocene origin related to a forced change of environment still has its adherents. Segerstråle (1977) suggested that the New and Old World freshwater *Pontoporeia* populations evolved independently from the (sub)arctic marine species *P. femorata* in connection with the last glaciations, as they were captured into continental ice-dammed lakes by the advancing arctic ice sheets; this argument was associated with the reestablishment of the North American freshwater populations as specifically distinct (*P. hoyi*) from the Eurasian lacustrine and brackish-water *P. affinis*.

Recently, Salemaa (1984, 1986) examined the karyology of *P. affinis* and *P. femorata*, and obtained chromosome counts $n = 26$ and $n = 14$, respectively. This led him to suggest that *P. affinis* arose from *P. femorata* through polyploidization. If so, a rapid divergence and even recurrent evolution of similar forms might be regarded as possible.

In this study, the relationships among the different *Pontoporeia* species are reassessed using enzyme electrophoresis. The degree of genetic divergence estimated by this method has generally been found to be roughly related to the time since the separation of evolutionary lineages (e.g. Thorpe 1982; Nei 1987); our results may thus be used to evaluate the different hypotheses on the phylogenetic relationships and the time involved in the evolution of the American and Eurasian freshwater *Pontoporeia* species and the marine *P. femorata*. Under the hypothesis of a polyploid nature of *P. affinis*, we can also examine another property related to the degree of evolutionary divergence, viz. the retention of duplicate gene expression after polyploidization.

Material and Methods

Species and Samples

Up to date, only three nominal species of *Pontoporeia* have been commonly recognized. Further taxonomic subdivision has long been anticipated, though, and the genus is currently undergoing a thorough revision, the first part of which is being published simultaneously with this study (Bousfield 1989; this is also leading to a reevaluation of the evolutionary history of the relict crustaceans on morphological grounds). However, the traditional treatment of taxa (e.g. Segerstråle 1937, 1977; Bousfield 1958) will still be followed here.

Pontoporeia femorata Kröyer, 1842, is a marine, arctic–boreal circumpolar taxon. In Europe, it is common in the northern waters of Norway and Iceland, and also on relatively deep (>30 m) soft bottoms of the Baltic Sea (e.g. Ekman 1953). We analyzed two samples: one from the northern Baltic Sea, off Tvärminne Zoological Station in southwestern Finland (salinity ca. 7‰), the other from the Tromsø area in northern Norway, from Nordkjosbotn of Balsfjorden (Fig. 1).

Pontoporeia affinis Lindström, 1855, is an inhabitant of North European lakes and arctic Eurasian estuaries. It also dominates in shallower and peripheral (less saline) areas of the Baltic Sea. We present data from Tvärminne, northern Baltic, where the species coexists with *P. femorata*. In addition to this locality, material has been examined from other areas of the Baltic (Bothnian Bay, Bothnian Sea, Gulf of Finland) and several Fennoscandian lakes (Fig. 1a). Most of the lakes were once isolated from the past (both fresh and brackish) phases of the Baltic basin in the course of postglacial land uplift, in the period 10 200–4000 BP.

FIG. 1. Sampling sites of *Pontoporeia* spp. (a) in Fennoscandia, (b) in eastern North America. The studied Fennoscandian lakes are Ärtingen, Mjörn, Ivösjön, Yxningen, and Båven (1–5) in Sweden, and Toisvesi, Iso Roinevesi, Päijänne, Saimaa, and Simpelejärvi (6–10) in Finland.

The North American freshwater populations are currently treated as *P. hoyi* Smith, 1874; until recently, they were usually regarded as conspecific with European *P. affinis*. Material from four lakes was examined for this study: L. George and Cayuga Lake, New York, and L. Mazinaw and Big Rideau Lake, Ontario. From L. Mazinaw, two samples were studied, one from about 100-m depth, the other from 25 m; the sites were 2 km

TABLE 1. Prevalent alleles (electromorphs) in *Pontoporeia* spp., and allele frequencies at polymorphic loci (in parentheses).

Locus	Species (and population)			
	affinis (Baltic)	"*affinis*" (St. Lawrence estuary)	*hoyi* (four lakes average)	*femorata* (Baltic)
Aco-1	*103* (.08) *100* (.92)	*107* (.10) *105* (.90)	*105*	*108* (.90) *105* (.10)
Ark-1	*100* (.88) *92* (.12)	*94*	*100*	*98*
Ark-2	*100*	*104*	*123*	*112* (.43) *104* (.57)
Gapd	*100*	*100*	*87*	*100*
Got-1	*100*	*100*	*108*	*120*
Got-2	*100*	*100*	*100*	*100*
Gpi	*100* (.56) *95* (.31) *90* (.13)	*95*	*112* (.04) *107* (.96)	*75* (.43) *65* (.57)
Gpt-1	*100*	*100*	*96*	*103*
Gpt-2	*108* (.35) *100* (.65)	*100*	*98*	*94*
Idh-1	*100*	*100*	*97*	*106*
Idh-2	*100*	*100*	*102*	*94*
Mdh-1	*100*	*100* (.71) *85* (.29)	*116*	*100*
Mdh-2	*100*	*100*	*100*	*90*
Mpi	*113* (.02) *106* (.52) *100* (.46)	*108* (.24) *102* (.76)	*113* (.34) *107* (.49) *100* (.17)	*108*
Pep-2	*100*	*108*	*97* (.19) *93* (.77) *89* (.04)	*115* (.13) *107* (.68) *85* (.19)
Pep-3	*103* (.03) *100* (.86) *93* (.11)	*88*	*108*	*82* (.03) *80* (.92) *74* (.05)
Pgd	*100*	*100* (.11) *93* (.89)	*106*	*97* (.85) *90* (.15)
Pgm	*103* (.04) *100* (.90) *94* (.03) *92* (.03)	*100*	*98* (.09) *94* (.91)	*97*
Tpi	*100*	*100*	*100*	*94*

apart. Different forms of mature males, of unknown taxonomical value, have been described from the North American freshwater populations (e.g. Segerstråle 1971); both *filicornis* and *brevicornis* type males were present in our material.

An *affinis*-like *Pontoporeia* is also present in North American coastal waters, often coexisting with *P. femorata* (e.g. Steele and Steele 1978; Bushdosh et al. 1982). Bousfield (1958) suggested that it may be specifically separable from the freshwater populations; here, it is designated *P. "affinis"*. One sample was examined, from Escoumins, Quebec, in the St. Lawrence estuary.

TABLE 2. Estimates of genetic identities *I* (below diagonal) and genetic distances *D* (above diagonal; SE in parentheses) for *Pontoporeia* spp.

	affinis	"*affinis*"	*hoyi*	*femorata*
P. affinis		0.48 (.18)	1.48 (.44)	1.73 (.53)
P. "affinis"	0.62		1.74 (.52)	1.59 (.44)
P. hoyi	0.23	0.18		2.76 (.90)
P. femorata	0.18	0.20	0.06	

Electrophoresis

The animals were usually frozen and stored at −70°C until analysis; also fresh specimens from Tvärminne, kept in aquaria, have been used for comparisons of *P. affinis* and *P. femorata*. Homogenates of whole animals were subjected to standard starch gel electrophoresis, followed by staining for specific enzymes (e.g. Harris and Hopkinson 1976).

Several buffer systems were screened to find the best running conditions for resolution of each enzyme. The most useful proved to be: (A) Tris-citrate pH 7.1 / 8.4 (Varvio-Aho and Pamilo 1980); (B) Tris-citrate-EDTA pH 7.1 (Ayala et al. 1974); (C) Tris-maleate pH 7.4 (1:1 dilution of the buffer in Shaw and Prasad 1970); (D) Tris-EDTA-borate pH 8.0 (Shaw and Prasad 1970); (E) morpholine-citrate pH 7.4 (Clayton and Tretiak 1972).

Allelic variation in all the examined species was scored from 19 loci, coding for the following 13 enzymes (in parentheses, the corresponding locus/loci, and the buffer system used): aconitase (*Aco-1*, A,E), arginine kinase (*Ark-1*, *-2*; C), glyceraldehyde-3-phosphate dehydrogenase (*Gapd*; B), glutamate-oxaloacetate transaminase (*Got-1*, *-2*; A), glucosephosphate isomerase (*Gpi*; B), glutamate-pyryvate transaminase (*Gpt-1*, *-2*; A), isocitrate dehydrogenase (*Idh-1*, *-2*; A), malate dehydrogenase (*Mdh-1*, *-2*; B), mannosephosphate isomerase (*Mpi*; A), peptidase, with leucyl-L-tyrosine as substrate in the staining reaction (*Pep-2*, *-3*; A), 6-phosphogluconate dehydrogenase (*Pgd*; E), phosphoglucomutase (*Pgm*; B), and triosephosphate isomerase (*Tpi*; B). The most common allele of *P. affinis* at each locus was denoted *100*; other alleles were named by adding to 100 the electrophoretic mobility difference (in millimetres) of the respective allozymes.

The activity of 13 additional enzymes could be reproducibly detected, but not reliably interpreted in terms of allelic variation in all the studied species. These enzymes, used only for comparing the number of isozyme loci expressed in *P. affinis* and *P. femorata*, were acid phosphatase (*Acp*; D), adenosine deaminase (*Ada*; D), aldehyde oxidase (*Ao*; D), NADH-diaphorase (*Dia*; A), esterase (with methyl-umbelliferyl acetate substrate) (*Est*; B,D), fructose-1,6,-diphosphatase (*Fdp*; A), β-glucuronidase (*Gus*; B), α-glycerophosphate dehydrogenase (α-*Gpd*; A), hexosaminidase (*Hex*; B), hexokinase (*Hk*; B,C), leucine aminopeptidase (*Lap*; D), pyruvate kinase (*Pk*; A), and sorbitol dehydrogenase (*Sor*; A).

Enzyme staining methods were mainly as in Harris and Hopkinson (1976); *Ark* was stained after Bulnheim and Scholl (1981).

Statistics

The degree of genetic differentiation between species was measured with Nei's indices of genetic identity *I* and standard genetic distance $D = -\log I$. *D* is an estimate of the number of (electrophoretically observable) gene substitutions per locus, provided that substitution rate is equal for all loci. The measure

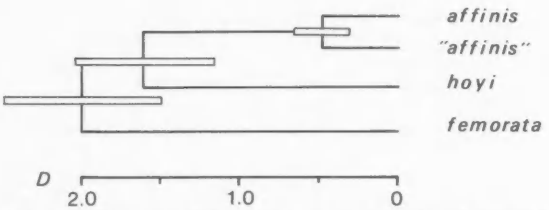

FIG. 2. Phenogram (UPGMA) of *Pontoporeia* spp. based on genetic distance estimates from 19 loci (Table 2). Boxes indicate ±1SE of the branching points (according to Nei et al. 1985).

$D_v = (1 - I)/I$ gives a better estimate when the rate varies among loci (e.g. Nei 1987). The distances were visualized as a phenogram constructed with the UPGMA method (Sneath and Sokal 1973); standard errors for branching points (assuming that the phenogram represents an estimate of phylogeny based on a regular substitution process) were calculated according to Nei et al. (1985). Gene frequency variation among conspecific populations was measured with F_{ST}, estimated following Weir and Cockerham (1984); this may be interpreted as an average standardized gene frequency variance at the polymorphic loci.

Results

Divergence among Taxa

All the three nominal species were highly differentiated from one another with respect to their allozyme genes. Of the 19 loci scored in all species, only 1–4 were undifferentiated or shared relatively common alleles in any pair of *P. affinis*, *P. hoyi*, and *P. femorata* (Table 1). This gives genetic identity estimates in the range $I = 0.06 - 0.23$, and corresponding genetic distances D ranging 1.5 to 2.8 (Table 2); in terms of D_v, all distances are higher than 3.3.

The North American coastal *P. "affinis"* was similarly distinct from *P. hoyi* and *P. femorata*, but more closely related to the European *P. affinis*; however, even these taxa were diagnostically different at six loci, and strongly differentiated, with alleles unique to one population, at further four of the loci. The genetic identity for this pair was estimated at 0.62, and distances D and D_v at 0.48 and 0.61, respectively.

Apart from the relatively close affinity of *P. affinis* and *P. "affinis"*, the data did not reveal any clear ranking of relationships among species. The greatest observed differentiation was between *P. hoyi* and *P. femorata*, but otherwise, character differences and similarities were distributed rather randomly among taxa and loci. The lack of resolution of the relative affinities among the nominal species is also illustrated by the standard errors of branching points in the phenogram interpreted as an estimate of phylogeny (Fig. 2).

Intraspecific Differentiation

The differentiation among populations initially regarded as conspecific was slight as compared with the interspecific variation, and did not involve diagnostic allelic differences. In terms of genetic distances, the intraspecific variation between lacustrine populations amounted to values not larger than $D = 0.02$, and generally much less. The strongest population differentiation was between the Baltic and Norwegian Sea *P. femorata*, with relatively great allele frequency differences at *Gpi* and *Ark-2* (Table 3); the average differentiation at six polymorphic loci can be characterized with $F_{ST} = 0.16$ (or $D = 0.022$, for 19 loci). For the four lake populations of *P. hoyi* (Table 4), $F_{ST} = 0.061$, and for eleven Fennoscandian *P. affinis* populations, including one from the Baltic, $F_{ST} = 0.060$ (detailed data for lacustrine *P. affinis* will be given elsewhere). The possible differences between the male morphs of *P. hoyi* are considered in the discussion.

TABLE 3. Allele frequencies at polymorphic loci in two *Pontoporeia femorata* samples. Sample sizes (number of studied individuals) in parentheses.

		Population	
Locus	Allele	Tvärminne, Northern Baltic Sea	Balsfjorden, Northern Norway
Aco-1	*108*	0.90	1.00
	105	0.10	—
		(83)	(14)
Ark-2	*112*	0.43	0.89
	104	0.57	0.11
		(122)	(28)
Gpi	*75*	0.43	0.79
	65	0.57	0.21
		(116)	(28)
Pep-2	*115*	0.13	—
	107	0.68	0.55
	85	0.19	0.45
		(86)	(28)
Pep-3	*85*	—	0.02
	82	0.03	0.11
	80	0.92	0.77
	74	0.05	0.11
		(36)	(28)
Pgd	*97*	0.85	0.78
	90	0.15	0.22
		(106)	(27)

TABLE 4. Allele frequencies in samples of *Pontoporeia hoyi*. Sample sizes in parentheses.

		Population				
				Big	Mazinaw	
Locus	Allele	George	Cayuga	Rideau	25 m	100 m
Gpi	*112*	0.03	0.05	0.08	—	—
	107	0.97	0.95	0.92	1.00	1.00
		(100)	(173)	(103)	(175)	(102)
Mpi	*118*	0.01	—	—	0.02	0.01
	113	0.21	0.27	0.29	0.57	0.56
	107	0.51	0.49	0.58	0.35	0.41
	100	0.26	0.23	0.12	0.06	0.03
	94	0.02	0.01	—	0.01	—
		(100)	(131)	(106)	(190)	(99)
Pep-2	*97*	0.29	0.19	0.13	0.18	0.14
	93	0.70	0.69	0.85	0.82	0.86
	89	0.01	0.12	0.02	—	—
		(96)	(177)	(106)	(196)	(100)
Pgm	*98*	0.01	0.11	0.11	0.16	0.13
	94	0.99	0.89	0.89	0.84	0.87
		(100)	(159)	(112)	(197)	(100)

Number of Expressed Isozyme Loci

The number of independent isozyme zones, and, by implication, the number of genes coding for a specific enzyme activity, were similar for all studied enzymes in *P. affinis* and *P. femorata*. Table 1 gives an account of the multiplicity of loci coding for the 13 enzymes reported there (two ACO zones and three PEP zones were detected in both species, but all were not scored). From the additional enzymes, *Ada, Gus, Sor, Fdp,* α-*Gpd, Hk, Pk,* and *Dia* seemed to be represented by a single locus each, *Lap* and *Acp* by two, and *Ao, Est,* and *Hex* by three. The electrophoretic phenotype of FDP was two-banded in *P. femorata*, and that of AO-3 in *P. affinis*, but as the variation of bands was not independent in presumed heterozygotes, they were interpreted as products of one locus only. Similarly, the three covarying zones of ADA (in both species) were attributed to a single locus. Of the enzymes encoded by two loci in *Pontoporeia*, at least ACO, GOT, IDH, and MDH are known to be coded for by two loci, responsible for separate mitochondrial and cytoplasmic isozymes, in most other animals also. Two zones of activity in the ARK and GPT reactions have also been found in several other crustaceans, as are multiple zones of PEP, LAP, ACP, and EST activity.

In conclusion, no clear traces of genome duplication in *P. affinis* were detected at the level of enzyme gene expression. No deviations in the number of expressed loci were noted in the other studied species, either, but not all enzymes were examined.

Adding up the scored and unscored enzyme zones considered as products of independent loci, 42 loci in all were observed. Although the possible intraspecific variation in the latter category could not always be interpreted, an interspecific difference of electrophoretic mobility was apparent for all these enzymes except α-GPD and AO-2. Assuming that the intraspecific gene diversity ($\bar{H}=0.11$) at the 19 scored loci is representative for all, we get as another estimate of the genetic identity of *P. affinis* and *P. femorata* from 42 loci $I=0.134$, and genetic distance $D=2.01$ (± 0.39), or $D_v=6.5$.

Discussion

Evolutionary Divergence among Species

From observations in other animal taxa, a rough linear relationship between genetic distance and the time since the divergence of linages has been suggested, with unit distance corresponding to, according to various authors, 5–20 million years (e.g. Thorpe 1982; Nei 1987). The application of such generalizations is certainly subject to several qualifications (large stochastic errors and biases due to differences in the substitution rate among loci and in sensitivity of methods in different laboratories, possible differences in the substitution process among taxonomic groups; see e.g. Grant 1987; Nei 1987), but distances might still provide a reasonable guide to the order of magnitude of the age of phylogenetic events also in crustaceans; for $D>1$, the resolution is expected to be poor, anyway.

Although the distances among the three currently recognised *Pontoporeia* species ($D=1.5$–2.8) seem to fall above the range of applicability of any linear time correlations, they suggest that the time since the divergence of these major groups should be measured in units of tens of millions of years. At this level, the allelic substitution process will be dominated by recurrent changes, and the role of homoplasy (due to the nature of the electrophoretic method) will grow significant; some of the similarities in this study (e.g. at *Mpi*) may actually not have been retained since the common ancestor, but represent parallelism by chance. The distance between the European *P. affinis* and the North American coastal *P. "affinis"* ($D=0.48$), on the other hand, may indicate an age of some millions of years since the divergence of these lineages; even this event may thus have predated the beginning of the Pleistocene (ca. 2 million years ago).

It may also be instructive to compare the present distance estimates with some earlier studies. Distances as high as those among the three nominal *Pontoporeia* species are seldom encountered within genera of other animal groups (e.g. Thorpe 1983). They are greater than the genetic distance between two subgenera of *Mysis* ($D=1.2$; Väinölä 1986), and fall in the range found among different genera of the family Gammaridae (Siegismund et al. 1985; Skadsheim and Siegismund 1986); however, many intrageneric distances were estimated equally high in that taxonomically controversial group.

The transoceanic divergence within the *P. affinis* — *"affinis"* lineage is comparable with that between several pairs of taxa of fishes and invertebrates separated by the Isthmus of Panama, the age of which is ca. 3.5 million years; these distances (reviewed by Grant 1987) mostly range from 0.11 to 0.64. The divergence in *Pontoporeia* is also at least as high as that among the three sympatric and reproductively isolated sibling species of the *Gammarus zaddachi* group in northwestern Europe ($D=0.20$–0.50), Siegismund et al. 1985), or that among the electrophoretically identified sibling species of the *M. relicta* group ($D=0.25$–0.38, Väinölä 1986). Divergence between morphologically recognised species of the (sub)genus *Mysis* measured $D=0.57$–0.79 in the same study. In the light of these comparisons, the European (*affinis*) and North American (*"affinis"*) populations can undoubtedly be regarded as two distinct though relatively closely related species. On the other hand, it may be noted that the trans-Atlantic differentiation in some other marine crustaceans does not involve diagnostic differences, and corresponds to D values less than 0.03 (R. Väinölä, unpubl. data).

Our results thus dispute all suggestions of relatively recent (Pleistocene or even Pliocene) relationships among the currently recognized three *Pontoporeia* species, which, in various forms, have been presented by the majority of authors dealing with the zoogeography of the glacial relicts. In relation to the most recent speculations on a divergence in connection with the latest glaciation (Segerstråle 1977; Salemaa 1984), the evolutionary time scale is expanded by up to three orders of magnitude.

As to the earlier views (up to 1950s), it may be noted that even though *P. affinis* was usually regarded as relatively recently derived from *P. femorata*, the morphological transition in this case was originally not considered a result of becoming (recurrently) isolated in novel freshwater environments, as was postulated for the evolution of *M. relicta* from *M. oculata*. Rather, the speciation in *Pontoporeia* was thought to have taken place in dilute northern seas, and the lacustrine populations were regarded as descendants of the arctic brackish-water *P. affinis* (e.g. Jägerskiöld 1912; Ekman 1918; Lomakina 1952; cf. also Ricker 1959; Dadswell 1974). This view was initially also accepted by Segerstråle (1957, 1962), who, unlike most others, also assumed that the descent of the Old and New World freshwater populations from Arctic Siberian ancestors was monophyletic. However, the recognition of the specific difference between *P. affinis* and *P. hoyi* led Segerstråle (1977)

to suggest that both freshwater species were directly derived from *P. femorata*, probably in connection with isolation into proglacial lake systems at the onset of the last glaciation.

Under this hypothesis, the present coastal populations were regarded, in turn, as descendants of the refugial glacial lake populations of the Weichselian/Wisconsinian period. This was also the postulated relationship for the North American *P. "affinis"* and *P. hoyi*; their close affinity was also conjectured by Ricker (1959) and Dadswell (1974). The ancient relationship of these species may thus seem the most unexpected result of this study. However, we note that the pattern and level of systematic subdivision implied by the genetic data (Fig. 2) is actually essentially in line with conclusions from more recent morphological studies (Bousfield 1989).

The strong differentiation among the main lineages also seems to support the view of Holmquist (1959, 1966) on an early divergence of the freshwater species from marine congeners. On the other hand, Holmquist regarded the relicts as coherent and stable species. This has proved not to be the case either for the freshwater *Pontoporeia* populations (Segerstråle 1977; this study), nor for *M. relicta* (Väinölä 1986). Yet, the evolutionary biogeography of the genus *Pontoporeia* turns out to be different from that of *Mysis*, where the freshwater populations (*M. relicta* group), albeit systematically subdivided into several sibling species, still constitute a distinct cluster in relation to the marine species (Väinölä 1986; R. Väinölä, B. J. Riddoch, R. D. Ward, and R. I. Jones, unpubl. data).

Intraspecific Differentiation

The differentiation observed within each of the taxa represents a level usually encountered within species, and does not warrant any further systematic subdivision. From geological considerations, the studied *P. hoyi* populations have been isolated from one another for a minimum of about 12 000 yr, and most of the Fennoscandian lakes for at least 8000 yr. Under a simple model of gene frequency evolution, population differentiation among initially identical, completely isolated populations will accumulate over generations through genetic drift at a rate $F_{ST}(t) = 1 - e^{-t/2Ne}$ (e.g. Nei 1987). Over such periods of time, and an assumed average generation interval of 2 yr, the observed level of differentiation ($F_{ST} = 0.06$) would be expected to arise in populations of a representative long term effective size N_e of the order 40 000 individuals due to stochastic factors alone. The geographical patterns of variation suggest, however, that part of the differentiation is probably older than the isolation of the lakes, and the actual postglacial effective sizes thus larger.

For the two *P. femorata* populations ($F_{ST} = 0.16$), the corresponding N_e would be somewhat lower. In the Baltic, *P. femorata* is considered a member in the "Arctic marine relict" faunal element, which has its main distribution in northern seas, but is practically absent from the intervening North Sea area. It is thought to have penetrated the Baltic basin after the final establishment of the marine connection through the Danish straits (ca. 8000 BP.) (e.g. Ekman 1953). In relation to the present abundance in the Baltic, the observed differentiation appears rather high; it could result from bottleneck(s) in connection with the colonization of the basin or in the fragmented Norwegian fjord environment. Similar levels of intraspecific differentiation have been found between conspecific Baltic and marine populations of some other crustaceans (Siegismund et al. 1985).

The differentiation between the Baltic and lacustrine *P. affinis* populations is not stronger than that among lakes on the average, not unexpectedly in view of the supposed late- and postglacial relationships of the populations (independent isolation of the lacustrine populations from a Baltic ancestral stock). Lomakina (1952) suggested a subspecific distinction between the lacustrine and brackish-water (both Baltic and Arctic estuarine) populations; however, this was not to postulate an existence of two monophyletic lineages, but in the spirit of the hypothesis of recurrent morphological evolution directed by the external environment.

Also at this level, we note a biogeographic difference between *Mysis* and *Pontoporeia*. The range of *P. affinis* in northern Europe, both in the Baltic and in lakes, overlaps those of two distributionally different species of the *M. relicta* group, which presumably also have different late-glacial colonization histories (Väinölä 1986; R. Väinölä, unpubl. data).

The North American populations studied here represent only a fraction of the total range of *P. hoyi*, which reaches up to the Mackenzie district in northern Canada, and involves populations derived from various refuge areas of the last glacial (Wisconsinian) period (e.g. Ricker 1959; Dadswell 1974). The easternmost refuge lakes are postulated to have existed in the Hudson River Valley (glacial Lake Albany; this could have contributed the Lake George population) and in the Genesee River headwaters (Salamanca reentrant; this was later transformed into a proglacial lake system involving the Cayuga basin) (Dadswell 1974). With the probable exception of Lake George, which was isolated first (Chapman 1937), our populations could also have been subject to an influence from a more western, Mississippian refugium stock, through upper Great Lakes connections before the final isolation of the studied lakes from the Lake Ontario basin (Lake Iroquois) ca. 12 000 BP. (cf. Prest 1970; Muller and Prest 1985). The two genetically most similar populations in our material were those of Cayuga Lake and Lake George. This could reflect a descent of these populations from only a single glacial ancestral stock (and thus a virtual absence of a contribution from a western gene pool in the Cayuga basin). On the other hand, somewhat stronger (random) genetic changes might have been associated with the colonization and isolation of the two other lakes, north of the present Lake Ontario; Lake Mazinaw was only briefly and marginally connected to the Ontario basin waters, whereas Big Rideau was probably influenced by the brackish Champlain Sea in the St. Lawrence valley (Dadswell 1974; Muller and Prest 1985).

Different Male Forms of *Pontoporeia hoyi*

The sexually mature males of *Pontoporeia* spp. are spectacularly different from female and juvenile individuals. They usually bear extensive antennal flagella, exceeding the body length, and strongly setose third uropods. Actually, due to these modifications, the males of all the three currently recognized species (*femorata, affinis, hoyi*) were once regarded as species of their own (*sinuata, weltneri, filicornis*; see Segerstråle 1937).

From several North American lakes, a neotenic male form is known, which exhibits some features of the normal fully developed male of *P. hoyi*, but resembles more the penultimate, incompletely developed stage with respect to other characters (Adamstone 1928; Segerstråle 1937, 1971; Henson 1954). This "*brevicornis*" male has conspicuously shorter antennal flagella (only ca. two-thirds of body length) than the "normal" ("*filicornis*") male, while it bears the completely developed

male characteristics on the seventh pereiopods and third uropods. The different male forms coexist in many lakes throughout the Great Lakes area (Segerstråle 1971).

The genetic background and taxonomic value of these forms are not known. They might represent alternative ontogenetic schemes determined solely by the environment, or be partially or completely under genetic control. At the other extreme, they might belong to separate biological species, hitherto unrecognised in juvenile and female individuals. If the male forms represented ancient, reproductively isolated lineages, they would probably be differentiated also with respect to randomly chosen marker genes.

In our material, collected in early July 1986, mature males were found in three lakes. The numbers of studied *filicornis* + *brevicornis* males were 14 + 21 in Cayuga Lake, 24 + 0 in Big Rideau Lake, 0 + 72 in Lake Mazinaw at 25 m, and 10 + 1 in Lake Mazinaw at 100 m. No diagnostic allozyme differences between the forms were detected, nor any general patterns of even slight frequency variation attributable to the male phenotypes. The unit of gene frequency evolution over the period involved in the generation of the among-lake variation has apparently been the geographical population, not the subpopulation defined by the male phenotypes.

However, a comparison of subsamples within lakes revealed a significant difference of *Mpi* frequencies between the *brevicornis* males of the 25 m Lake Mazinaw sample and the entire 100-m sample ($X^2_{(2)} = 8.85$, $P < 0.02$; the difference between the shallow and deep subsamples as such was not significant). If real, this intralacustrine differentiation (which was much weaker than that among lakes: $F_{ST} = 0.008$ versus 0.086, for *Mpi* alone) could reflect potential for effective isolation on a very local scale.

Although the data suggest that the male forms do not, in the long run, constitute independent lineages which should be treated as evolutionary and taxonomic entities, no light was shed on the possible involvement of genetic factors in the determination of the final phenotype. For the present, even a primarily environmental control remains a viable hypothesis. In our material from Lake Mazinaw, the occurrence of the two male forms was related to depth; a similar distribution is also known from Cayuga Lake (E. L. Bousfield, pers. comm.). For instance, it is possible that at higher summer temperatures (shallower sites) the development of the primary sexual characteristics is faster than that of the secondary sexual traits. An environmental control of the final morphological phenotype has been documented in some other amphipods (e.g. Sheader 1975).

Polyploidy in the Evolution of *Pontoporeia affinis*?

Polyploidization was considered as the only plausible mechanism for a rapid and recurrent origin of the freshwater "relict" species from presumed marine ancestors already by Holmquist (1959: chapter 4, 1966); however, she rejected this hypothesis on the basis of karyological studies on *Mysis*. More recently, the chromosome counts of Baltic *P. femorata* ($n = 14$) and *P. affinis* ($n = 26$) led Salemaa (1984, 1986) to suggest, in the spirit of Segerstråle's (1977) hypothesis of a recent ancestor–descendant relationship between these species, that *P. affinis* arose from *P. femorata* via tetraploidization in connection with the last ice ages. (Other mechanisms for such karyological differentiation would have seemed unlikely, as the rate of chromosomal evolution in amphipods has generally been cited as low; haploid numbers in studied species tend to concentrate around a modal $n = 26$ (!) (Orian and Callan 1957; Niiyama 1959). On the other hand, great variation in chromosome numbers, suspected as a result of polyploidization, has recently also been found among *Gammarus* species (Amphipoda) in the ancient Lake Ohrid (Salemaa 1985)). Although our results on the degree of allozyme differentiation indicate that the evolutionary divergence of *Pontoporeia* spp. was far more ancient than that assumed by Segerstråle and Salemaa, this as much does not rule out the possibility of a tetraploidization event at some stage of the evolution of the *P. affinis* lineage.

When a tetraploid lineage arises, all the genes of the original genome(s) will initially be duplicated. However, as the multiple dose of genes is usually not necessary for the organism, deleterious or harmful alleles may accumulate through mutation and genetic drift in the tetraploid genome as long as one of each of the replicate loci remains functional. The gradual loss of duplicate gene expression through this process has received much attention both from theoreticians (e.g. Li 1980, 1982; Watterson 1983) and students of isozyme expression of (presumably) tetraploid organisms (e.g. Allendorf et al. 1975; Ferris and Whitt 1977a,b; Soltis and Soltis 1988). We did not find any evidence of retained duplicate gene expression in *P. affinis*. In the light of the theoretical and empirical background (reviewed by Li 1982), it may be asked whether this constitutes valid evidence against a tetraploid origin of *P. affinis*, or whether a loss of all signs of the hypothesized polyploidization at this level could be expected.

In theoretical models, the rate of loss of duplicate gene expression depends on the mutation rate to nonfunctional alleles (μ), selection against heterozygotes (s), and effective population size (N_e). The available estimates for the null mutation rate, though crude, are mostly of the order $\mu = 10^{-6}$–10^{-5} per generation (see Li 1982). For such mutation rates and reasonably large population sizes, the average time for gene silencing will be primarily governed by population size, and be of the order $10\,N_e$ (Li 1980; Watterson 1983). With a generation interval of 1–3 yr and long term N_e's of even one or a few million individuals, these models predict that some retained duplicated expression should be detected still after some tens of million years; this would not appear an improbable situation (species N_e), considering the present population densities (often thousands per square metre) and wide distribution of *P. affinis*. Even with effective population sizes of the order 10^5 (which may be realistic for some local populations, cf. above) detectable duplicate activity would be retained for some millions of years.

From empirical data, the realized rate of gene silencing seems to be even slower, and a total loss of duplicate expression thus more unlikely even in older tetraploid lineages. The most extensive results concern several fish families (Salmonidae, Catostomidae, Cobitidae, Cyprinidae), where genome duplication may date back to 15–100 million years ago. These taxa still retain duplicate expression at 25–50% of isozyme loci (review in Li 1982). If the evolutionary dynamics of the *Pontoporeia* genome is similar to that in fishes, a relatively high level of duplicate gene expression would be expected, as the maximum time since the postulated polyploidization probably falls in the range cited for fish, and the population sizes of amphipods are hardly smaller than those of fish.

In conclusion, in the light of these comparisons it is evident that *P. affinis* did not arise through polyploidization in connection with late Pleistocene glaciations, as suggested by Salemaa (1984). The data give no support for a polyploidization event earlier in the history of the *P. affinis* lineage, either, although

such a hypothesis probably cannot be conclusively rejected. The great difference in the chromosome numbers of *P. affinis* and *P. femorata* might better be taken as further evidence of their distant evolutionary relationship.

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Revised Morphological Relationships Within the Amphipod Genera *Pontoporeia* and *Gammaracanthus* and the "Glacial Relict" Significance of their Postglacial Distributions

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The Holarctic coastal marine and freshwater members of the amphipod families Pontoporeiidae and Gammaracanthidae reveal much greater taxonomical, distributional–ecological, and physiological diversity than formerly recognized. *Pontoporeia* is formally divided into three full genera (comprising more than 20 species), namely, *Pontoporeia* (Kroyer, 1842; ***Monoporeia***, new genus, and ***Diporeia***, new genus. *Gammaracanthus* is divided into two full genera (encompassing about a dozen species) namely, *Gammaracanthus* Bate, 1862, and ***Relictacanthus***, new genus; *Gammaracanthus* is divided into the subgenera *Gammaracanthus* Bate, and ***Pseudacanthus***, new subgenus. The genera are transferred from family Gammaridae, superfamily Gammaroidea, to family ***Gammaracanthidae*** (newly diagnosed herein) within superfamily Eusiroidea. Two lines of evidence refute previous theories (e.g. Hogbom's "sluicing up" theory) concerning the origin and evolution of the so called glacial and marine–glacial crustacean fauna of the northern hemisphere: (1) the broad taxonomic diversity of pontoporeiid and gammaracanthid amphipods; and (2) the regional endemicity of primary freshwater members of Eurasia and North America, between which no intercontinental exchange apparently took place during Pleistocene and recent times. A more credible explanation for such taxonomic and biogeographical diversity requires a much longer time frame (e.g. late Cretaceous to late Tertiary times).

L'étude des amphipodes de la famille des Pontoporeiidae et de la famille des Gammaracanthidea qu'on trouve dans les eaux douces et dans les eaux côtières holarcituqes montre que ces organismes sont beaucoup plus diversifiés au point de vue de leur taxonomie, de leur distribution, de leur écologie et de leur physiologie qu'on ne l'avait d'abord cru. *Pontoporeia* se divise en trois genres reconnus à part entière (qui regroupent plus de 20 espèces), soit *Pontoporeia* Kroyer, 1842; ***Monoporeia***, un nouveau genre, et ***Diporeia***, également un nouveau genre. *Gammaracanthus* se divise en deux genres à part entière (regroupant environ une douzaine d'espèces), soit *Gammaracanthus* Bate, 1862 et ***Relictacanthus***, un nouveau genre; *Gammaracanthus* comprend le sous-genre *Gammaracanthus* Bate et le nouveau sous-genre ***Pseudacanthus***. Ces genres, autrefois classés dans la famille des Gammaridae, de la superfamille des Gammaroidae, sont maintenant classés dans la famille des ***Gammaracanthidea*** (nouvelle diagnose présentée ici), de la superfamille des Eusiroidae. Les données infirment de deux façons les théories avancées jusqu'ici (p. ex. celle de Hogbom) quant à l'origine et à l'évolution des crustacés dits glaciaires et marins-glaciaires de l'hémisphère nord : (1) la grande diversité taxonomique des Pontoporeiidae et des Gammaracanthidae; (2) le fait que les organismes d'eau douce primaires soient régionalement endémiques en Eurasie et en Amérique du Nord, deux régions entre lesquelles il ne s'est apparemment produit aucun échange durant le pléistocène et l'époque actuelle. Pour expliquer de façon plus vraisemblable une telle divjersité taxonomique et biogéographique, il faut considérer une période de temps beaucoup plus longue (p. ex. du crétacé supérieur au tertiaire supérieur).

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The "glaciomarine relict," or "glacial relict" idea of Loven (1861) applied to organisms that are now confined to continental freshwater basins resulting from Pleistocene glaciation. These organisms include certain amphipod crustaceans ascribed to *Pontoporeia affinis* and *Gammaracanthus loricatus* and their varieties (see Bousfield 1958; Segerstrale 1962, 1966; Dadswell 1974). According to Hogbom (1917) and later authors (e.g. Ricker 1959; Segerstrale 1962; Dadswell 1974) their origin is explained by marine inundations of coastal regions and subsequent entrapment in freshening ponds, or by the proglacial "sluicing up" theory of Hogbom (1917). The latter postulated, mainly, that coastal marine and brackish-water populations had become trapped by advancing marine glacial ice sheets, and were pushed slowly but progressively landwards by Pleistocene glacial expansion. During prolonged periods of glacial maxima, the animals became functionally acclimatized and genetically stable within continental freshwater environments. Evidence supporting chromosomal polyploidy as a possible mechanism for rapid (Pleistocene) evolution of glacial relict species was suggested by Salemaa (1986).

Subsequent to Hogbom, some authors noted considerable species diversity among the so called relicts, and began to express reservations about the validity of his thesis. Thus, Holmquist (1959) revealed a diversity of species within the *Mysis relicta–oculata* complex, often used as classical support for the Hogbom thesis, that must have existed for a considerable

period and implied an origin much earlier than Pleistocene. From electrophoretic enzyme analysis of fresh material, Vainola and Varvio (1989) categorically rejected the role of the Ice Ages in moulding the currently recognized systematic structure of the genus *Pontoporeia*. Both Holmquist (1959) and Vainola and Varvio (1989) rejected also the polyploidy explanation for rapid evolution of component species of *Pontoporeia* and other glacial relict crustaceans within Pleistocene and recent times.

This study summarizes recently discovered taxonomic and ecological–distributional diversity within the Holarctic amphipod genera *Pontoporeia* and *Gammaracanthus*, based on gross morphology (E. L. Bousfield, unpubl. data). It relates the modern distributions of component species to aquatic refugial areas of the Pleistocene glacial maxima, and outlines alternative scenarios that more realistically account for the high taxonomic diversities and mutually exclusive distributions observed here.

Systematics

A formal taxonomic reassessment of gammaridean amphipod groups used in this study is required at this time, partly to validate the new taxonomic names, and partly to reaffirm their correct phyletic relationships at family and superfamily levels. The following diagnoses apply to the mature female sex, unless otherwise stated. Females are generally larger, continuously benthic, and longer-lived (mature males are often pelagic, short-lived), and thus more commonly encountered in field samples.

Within superfamilly Pontoporeioidea and family Pontoporeiidae (sensu Bousfield 1982a, 1983) the old genus *Pontoporeia* Kroyer, 1842, contains about 22 species that have been previously established by others, or are being newly described elsewhere (E. L. Bousfield, unpubl. data). A formal subdivision of Kroyer's old generic concept into three distinct genera is proposed below.

Family Pontoporeiidae Sars, 1882

Haustoriidae Stebbing, 1906: 118 (*partim*).
Haustoriidae Gurjanova, 1951: 328 (*partim*).
Haustoriidae (Pontoporeiinae) Bousfield, 1965: 166 (*partim*).
Pontoporeiidae Bousfield, 1979: 358; 1982a: 258.
Gammaridan: Pontoporeiids Barnard and Barnard, 1983: 562 (*partim*).

Generic content:
Pontoporeia Kroyer, 1842, (TYPE genus)
Monoporeia, new genus (this page)
Diporeia, new genus (p. 1680)
Priscillina Stebbing, 1888.
Amphiporeia Shoemaker, 1929.
Bathyporeia Lindstrom, 1855.

Taxonomic commentary:

Sars' (1882) original concept of the family has been more narrowly defined to exclude all but the genotype and closely related genera of the North Atlantic and Holarctic regions (above). Barnard and Barnard (1983) have incorrectly included within the pontoporeiid complex the eusiroidean austral genus *Zaramilla* (Stebbing, 1888). They have also incorrectly submerged the pontoporeiids within, but correctly excluded the haustorioids from, the Gammaroidea. The Pontoporeiidae is excluded from the Gammaroidea (*Gammarus*: TYPE genus) by several major character differences previously outlined by Bousfield (1979, 1982a, 1983). These include: (1) differing reproductive life styles (pontoporeiids have a pelagic mating system, gammaroideans have a benthic preamplexing system, sensu Borowsky 1984); (2) differing antennal sensory structures (pontoporeiids have calceolate antennae 1 and 2, but only in males; in gammaroideans (with the exception of a few *Micruropus* of Lake Baikal) calceoli are restricted to antenna 2, of both males and females); and (3) pontoporeiids lack the coxal gill that is present on peraeopod 7 in nearly all true gammaroideans.

Genus *Pontoporeia* Kroyer, 1842, (Figs. 1A,E,F;2A)
Pontoporeia Stebbing, 1906: 127 (*partim*)
Pontoporeia Gurjanova, 1951: 345 (*partim*)
Pontoporeia Barnard, 1969: 258 (*partim*)
Pontoporeia Barnard and Barnard, 1983: 563 (*partim*)

Species content:
Pontoporeia femorata Kroyer, 1842. (TYPE species)
Pontoporeia ekmani Bulycheva, 1936.
Four new species, based on material from Holarctic (especially Canadian arctic) coastal marine regions, to be described (E. L. Bousfield, unpubl. data).

Diagnosis:

Urosome segment 1 with distinct dorsal tooth or bifid process (reduced in male). Lateral head lobe strongly produced, acute. Antenna 1, accessory flagellum short, 2-segmented (female), antenna 2 peduncular segments 4 and 5 with two to three lateral facial fanwise groups of spines, segment 5 with spinose antero–distal process.

Gnathopod 1, propod hatchet-shaped, palm lacking postero–distal spines; carpus, hind lobe deep, narrow (Fig. 2A). Gnathopod 2, weakly parachelate; propod elongate, nearly equal in length to carpus; palm with group of three postero–distal spines.

Coxa 4 not (or very shallowly) excavate behind. Coxa 5 deeply antero–lobate, anterior lobe aubacute, nearly as deep as coxa 4. Bases of peraeopods 5 and 6 subequal in depth.

Uropods 1 and 2, both margins of rami lined with short slender spines. Uropod 3, rami elongate (2× peduncle), outer ramus with small but distinct terminal segment. Telson longer than wide, lobes fused in basally (one-third), apices with two to three short spines. Sternal gills lacking.

Distribution:

Holarctic, coastal marine (shelf) waters, southward in the North Pacific and North Atlantic to the limit of summercold (<10°C) temperatures.

Monoporeia, new genus (Fig. 1C, 2B)
Pontoporeia Gurjanova, 1951: 345 (*partim*)
Pontoporeia Barnard and Barnard (1983): 563 (*partim*)

Species content:
Monoporeia affinis (Lindstrom, 1855) (TYPE species)
Monoporeia gurjanovae (Birula, 1937)
Monoporeia microphthalma (Sars, 1896)
Two new species based on material from inshore and estuarine Holarctic (Canadian Arctic and Bering Sea) regions, to be described (E. L. Bousfield, unpubl. data).

Diagnosis:

Urosome 1 with weak dorsal hump (not bifid) (Fig. 1C). Lateral head lobe normal, subacute. Antenna 1, accessory flagellum 3–5 segmented. Antenna 2, peduncular segments 4 and 5 broader, length 1–2× breadth, each with one major fanwise group of lateral facial spines; segment 5 with small, spinose antero–distal process.

Gnathopod 1, propod ovate, convex palm smoothly continuous with posterior margin; carpus longer than deep, hind lobe

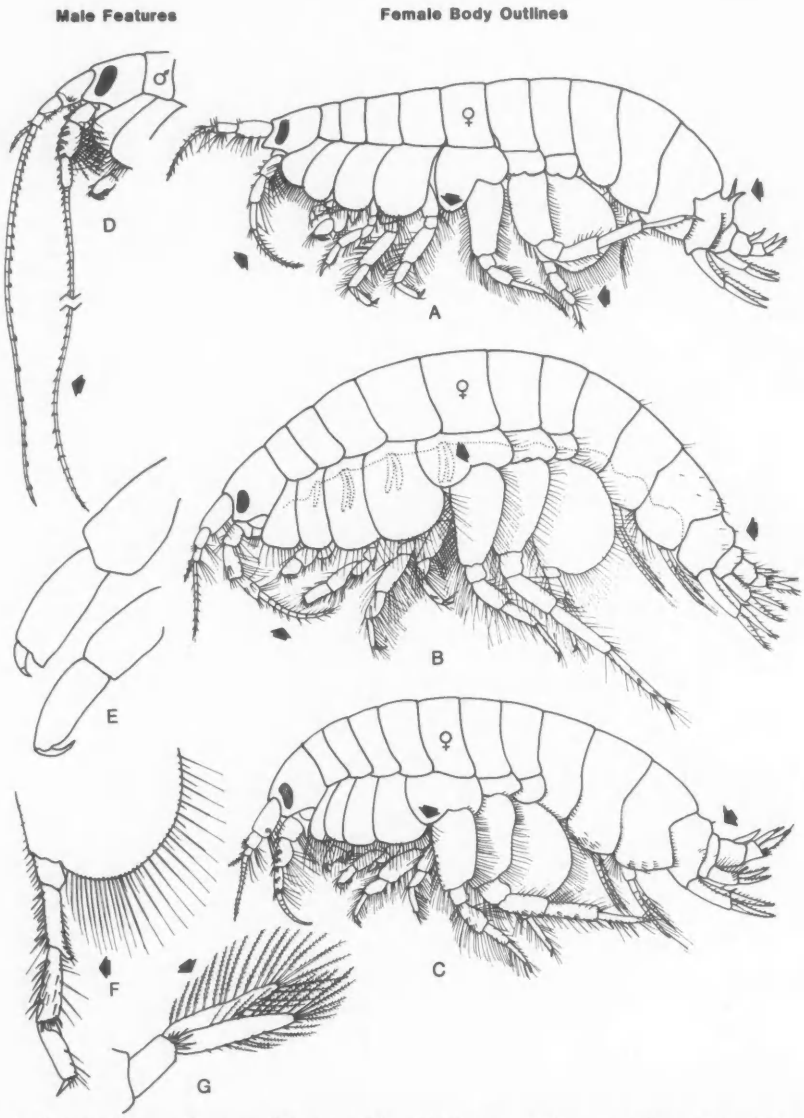

FIG. 1. Lateral views of genera of Pontoporeiidae. (A) *Pontoporeia femorata* (Kroyer). Female body outline, (B) *Diporeia*, n.g. (*filicornis* group). Female body outline, (C) *Monoporeia*, n. g (*affinis* group). Female body outline, (D) *Diporeia*, n.g. (*filicornis* group). Male head region, (E) *Pontoporeia femorata* (Kroyer). Male, gnathopods 1 and 2, distal segments (carpus, propod, and dactyl), (F) *Pontoporeia femorata* (Kroyer). Male, peraeopod 7, distal segments, (G) *Diporeia*, n.g. (*filicornis* group). Male, uropod 3.

medium-deep, squared below (Fig. 2B). Gnathopod 2 weakly subchelate; propod short, about half length of carpus; palm small, posterior angle with pair of short spines and two to three long plumose slender spines.

Coxa 4 weakly excavate behind. Coxa 5 weakly antero–lobate, anterior lobe rounded below. Basis of peraeopod 5 shorter than in 6.

Uropods 1 and 2, rami sparsely spinose, spines lacking on outer margins. Uropod 3, rami short, <1 1/2× length of peduncle; outer ramus with vestigial (barely visible) terminal segment.

Telson short, wider than long; lobes fused basally (one-half), apices each with several slender spines. Sternal gills (when present) median finger-like processes on peraeon segments 2–5.
Distribution:

Holarctic, coastal marine, mainly brackish lakes and estuaries, and marine-glacial relict lakes, especially of the Fennoscandia and Karalian regions, and the Kamtchatka peninsula.

Diporeia, new genus (Figs. 1B,D; 2C,G)

Pontoporeia Gurjanova (1951): 345 (*partim*)

Pontoporeia Barnard and Barnard (1983): 563 (*partim*)

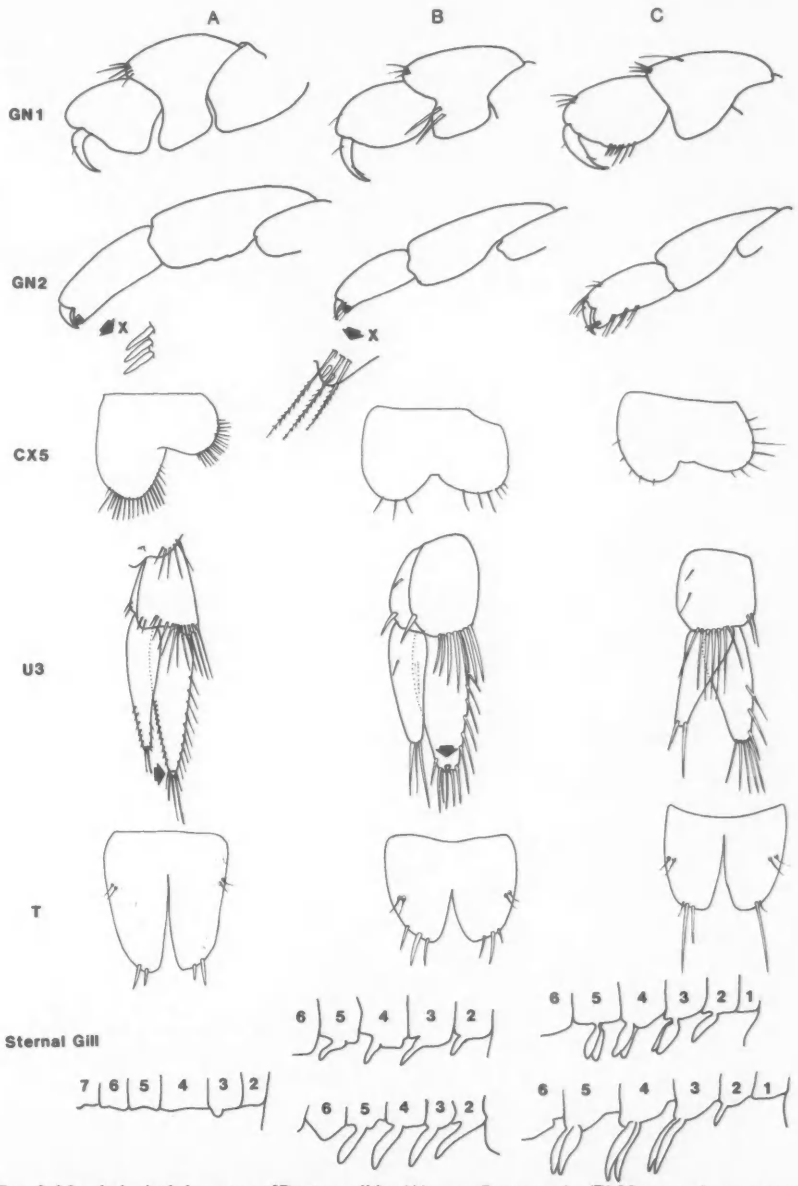

FIG. 2. Morphological characters of Pontoporeiidae (A) genus *Pontoporeia*, (B) *Monoporeia*, new genus, (C) *Diporeia* new genus. GN1; gnathopod 1, GN2; gnathopod 2, CX5; coxal plate of peraeopod 5, U3; uropod 3, T; telson, Sternal gill; sternal gills on sternum of peraeonal segments 2–5.

Species content:

Diporeia hoyi (Smith, 1874) (TYPE species)
Diporeia filicornis (Smith, 1874)
Diporeia kendalli (Norton, 1909)
Diporeia erythrophthalma (Waldron, 1953)
Diporeia brevicornis (Segerstrale, 1937)
Diporeia intermedia (Segerstrale, 1977)
Two new species (*brevicornis* group) from the Great Lakes system, to be described (E. L. Bousfield, unpubl. data).

Diagnosis:

Urosome 1 with weak dorsal hump (or lacking); posterior pleosome and urosome often dorsally setulose (Fig. 1B). Lateral head lobe not produced, subacute. Antenna 1, accessory flagellum 3–4 segmented. Antenna 2, peduncular segments 4 and 5 normal, with one major fanwise group of lateral facial spines; segment 5, antero–distal process very weak, spine group weak.

Gnathopod 1, propod deeply ovate; palm with group of three postero–distal spines; carpus longer than deep, hind lobe shallow, unevenly rounded below. Gnathopod 2 weakly parachelate; propod medium, about two-thirds length of carpus; palm relatively strong, postero–distal angle with two to three spines.

Coxa 4 distinctly excavate behind. Coxa 5 shallow, almost aequilobate, anterior lobe rounded below. Basis of peraeopod 5 longer (deeper) than basis of peraeopod 6.

Uropod 1, rami sparsely spinose, especially outer margin of inner ramus. Uropod 2, rami with long slender marginal spines except on inner margin of outer ramus. Uropod 3, rami short, outer ramus lacking terminal segment.

Telson squared, about as wide as long, lobes cleft to base, apices with long and short slender spines. Sternal gills double on peraeon segments 3–5, single on segment 2.

Taxonomic commentary:

Species of Diporeia form two natural groupings, possibly of subgeneric significance[1]: (1) a *filicornis* group (*D. hoyi, D. filicornis, D. kendalli*, and *D. erythrophthalma*) having elongate antennae (flagellum 40–65 segments) and large, fully setose calceolate uropod 3 in the male; (2) a *brevicornis* group (*D. brevicornis, D. intermedia*, and two new species) having short antennae (flagellum 18–35 segments) and relatively small, weakly setose uropod 3 in the male.

Distribution:

All known species are confined to deep, summer-cold continental, glacial relict lakes of North America.

Superfamily Eusiroidea Bousfield, 1979
Gammaracanthidae, new family

Gammaridae Barnard, 1969: 231 (*partim*)
Acanthogammaridae Bousfield, 1977: 294 (*partim*) 1982a: 260 (*partim*)
Acanthogammarids Barnard and Barnard, 1982: 520 (*partim*)
Gammaracanthidae Bousfield, 1984 MS

Generic content:

Gammaracanthus (Gammaracanthus) Bate, 1862, (TYPE genus and subgenus)
Gammaracanthus (Pseudacanthus), new subgenus, p. 1682.
Relictacanthus, new genus, p. 1683

Diagnosis:

Body large, slender to medium width, strongly carinate middorsally on pleon, urosome, and posterior peraeon. Rostrum very strong, acute. Inferior head lobe produced ventro-laterally. Eyes large, protruding from head surface. Antennae slender (first longer), lacking calceoli. Accessory flagellum well developed.

Mouthparts eusiroidean. Upper lip notched medially. Lower lip, inner lobes well developed. Mandible, molar triturative; blades slender; right lacinia bifid or trifid; palp elongate. Maxilla 1, outer plate with seven to 10 apical spines; inner plate short, setose. Maxilla 2, inner plate with strong facial row of setae. Maxilliped strong, palp raptorial; outer plate short, medially spinose; inner plate short, basally setose.

Coxal plates 1–4 shallow to medium depth, vertically ribbed; coxa 4 weakly (or not) excavate behind. Gnathopods large, powerfully subchelate, raptorial, "eusiroidean" in form (carpus longer than deep, posterior lobe small, narrow); propod palms smooth, convex, postero–distal angle with groups of stout spines.

Peraeopods slender, weakly spinose (rarely setose); segment 6 not longer than 5; dactyls short. Peraeopods 5–7 elongate, subsimilar in form but markedly differing in size (6 longest, 5 shortest); coxa 5 anterolobate, 6 posterolobate, lobes narrowing below.

Pleon plates broad, deep, hind corners acuminate. Pleopods strong, rami elongate; pleopod 2 usually sexually dimorphic. Uropods 1 and 2 short, stout, rami with apical spines. Uropod 3 large, rami paddle-shaped, subequal, margins plumose-setose. Telson short, broad, lobes separated nearly to base.

Coxal gills large, double-plated, on peraeopods 2–7. Midventral sternal gills occasionally present on peraeon segments 2–7 and pleon segment 1. Brood lamellae very large, broad, margins with numerous simple setae.

Males smaller and more slender than females. Penis papillae large, rod-like.

Taxonomic commentary:

Within the Eusiroidea, the Gammaracanthidae has strongest affinity with the *Epimeria* group of Paramphithoidae, the Amathillopsidae, and to lesser extent, the Eusiridae.

Distribution:

Holarctic marine, brackish, and Eurasian freshwater.

Genus *Gammaracanthus* Bate, 1862

Gammaracanthus Bate, 1862: 201
Gammaracanthus Stebbing 1906: 507 (*partim*)
Gammaracanthus Gurjanova 1951: 784 (*partim*)
Gammaracanthus Barnard 1969: 241 (*partim*)
Gammaracanthus Bousfield, 1984: MS (*partim*)

Subgeneric content:

Gammaracanthus (Gammaracanthus) Bate, 1862 - NOMINATE subgenus (p. 1682).
Gammaracanthus (Pseudacanthus), new subgenus (p. 1682)

Diagnosis:

Rostrum decurved distally, extending to about tip of peduncle 1, antenna 1. Inferior head lobe medium to strong, produced laterally by at least its basal width. Antenna 1, peduncular segments 2 and 3 progressively shorter than 1, 3 about half segment 1. Antenna 2, peduncular segment 5 shorter than segment 4; flagellum equal to, or longer than peduncle 5.

Mouthparts relatively strongly modified. Mandible, palp segment 3 fully with elongate terminal setae; spine-row with few (5–10) blades. Maxilla 1, outer plate with 7–11 apical spines; palp with simple marginal setae.

Coxal plates 1–4 medium deep, increasing uniformly posteriorly. Gnathopods unequal in size (2 larger), or subequal, subsimilar in form; bases with posterior marginal clusters of "comb-setae," and isolated long simple setae. Gnathopod 1, carpus not longer than in gnathopod 2; propod broadest proximally, hind margin short, postero–distal angle with three to four groups of medium to short spines; distal (postdepression) palmar spine group lacking (setae only).

Peraeopods stout, spinose. Peraeopods 3 and 4 closely subequal in length. Peraeopods 5–7 bases medium broad, little differing in length and form, hind margin proximally rounded; segment 5 (of peraeopods 5 and 6) slightly longer than segment 6.

Pleon plates strongly acuminate and/or produced posteriorly. Pleopod 2 sexually dimorphic; inner ramus elongate, distal segments short-spinose and lacking plumose swimming setae in

[1]Vainola and Varvio (1989, p. 18) describe the male of 'brevicornis' as a neotenic form of the normal, fully developed male of *P. hoyi* ('*filicornis*' group). Such was found not to be the case in the present study. In the mature male of species of the '*brevicornis*' group included here (Bousfield, in prep. I), all characters are those of a fully mature male instar. Moreover, the '*brevicornis*' species possess penultimate and anti-penultimate male instars that correspond closely to those of the '*longicornis*' (*hoyi*) group. Also, ovigerous females of at least one species of the '*brevicornis*' group are taxonomically distinguishable from females of the '*longicornis*' group.

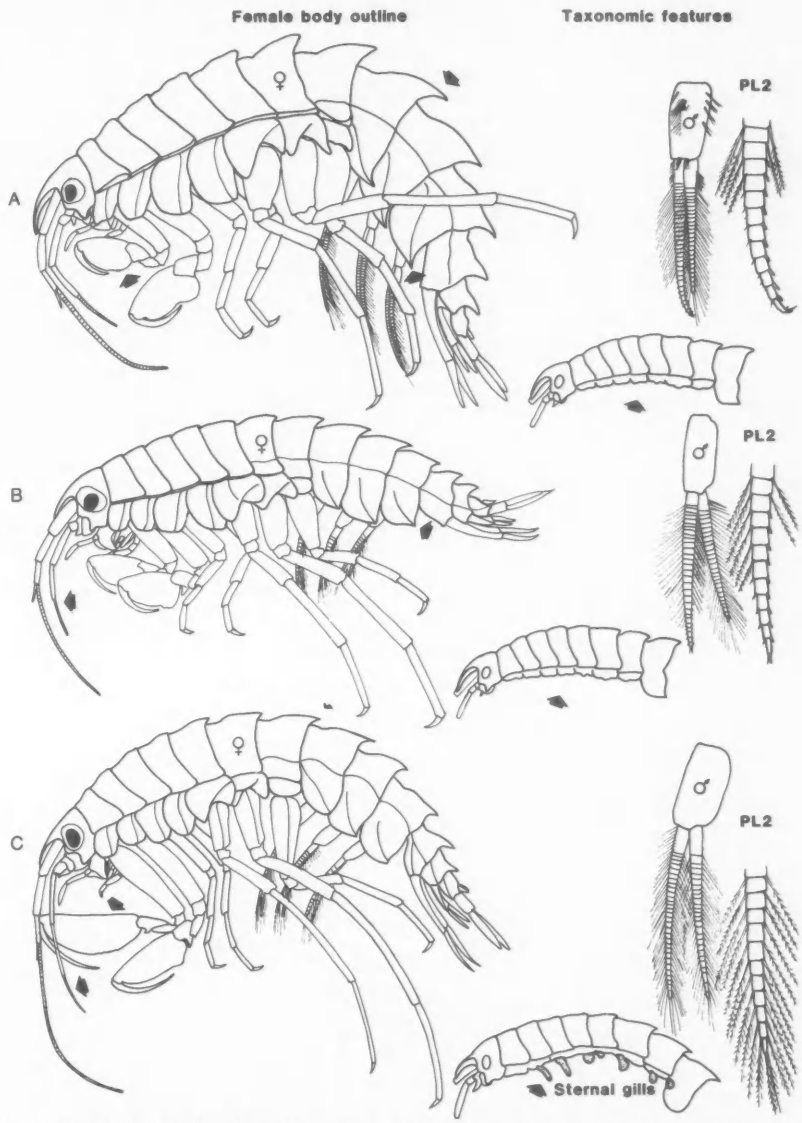

FIG. 3. Morphological characters of Gammaracanthidae (A) genus *Gammaracanthus*, subgenus *Gammaracanthus*. Female lateral body outline, (B) genus *Gammaracanthus*, subgenus *Pseudacanthus*. Female lateral body outline, (C) *Relictacanthus*, new genus. Female lateral body outline. Insets: (1) lateral body outline (female) showing sternal plates and sternal gills (when present), (2) pleopod 2 (male), and enlarged distal portion of inner ramus (subinset).

male. Uropods 1 and 2, rami distinctly shorter than respective peduncles. Uropod 3, rami broadly paddle-shaped, length about 4× width. Telson lobes separated basally with a few subapical lateral setae. Sternal gills lacking.

Distribution:

Holarctic; coastal marine and brackish waters, estuaries, and marine-glacial relict lakes.

Gammaracanthus (Gammaracanthus) Bate, 1862 (Fig. 3A)

Species Composition:

Gammaracanthus loricatus (Sabine, 1821) (TYPE species)

Four new species from North American arctic marine localities, to be described (E. L. Bousfield, unpubl. data).

Diagnosis:

Body carinated strongly on peraeon 5–7 and pleon 1–5. Lateral ridges above coxal plates 1–7, dorso–lateral ridge on peraeon (5)6 and pleon 1–4 strongly demarcated. Rostrum extending to or beyond tip of peduncle 1, antenna 1. Inferior head lobe strong, acute, produced laterally by more than its basal width. Antenna 1, accessory flagellum 4-segmented. Antenna 2, flagellum longer than peduncle 5, 14+ segmented.

Mandible, palp segment 3 with several elongate terminal setae; spine-row short (five to nine blades). Maxilla 1, outer plate with 10 apical spines; palp with simple marginal setae.

Coxal plates 1–4 large, deeper than corresponding peraeonal segments, increasing uniformly posteriorly, prominently ribbed. Gnathopods unequal in size (2 larger) but subsimilar in form; Gnathopod 1, hind margin of propod short, convex; postero–distal angle with three to four spine groups, each with three to four medium to short spines, distal spine group lacking (setae only). Gnathopod 2, propod relatively deep (80% of length), proximally broadest; postero–distal angle with five spine groups, distal three groups with 3–7 medium spines.

Peraeopods relatively stout. Peraeopods 3 and 4, bases subequal in length to coxal plates. Peraeopods 5–7 unequal in length; peraeopod 6 much the longest, 7 smallest, slightly shorter than 5, bases little differing in length and form. Coxae of peraeopods 5 and 6, lobes acute.

Pleon plates 1–3 cuminate and strongly produced posteriorly. Pleopod 2 strongly sexually dimorphic; inner ramus elongate, distal nine to 11 segments short-spinose, lacking plumose swimming setae.

Taxonomic commentary:

The five species of this group exhibit considerable morphological diversity of body form, rostral length, and gnathopod structure (E. L. Bousfield, unpubl. data).

Distribution:

All species are fully marine along Holarctic coastlines, seldom occuring in estuarine conditions (salinities <20‰); members of one species are disjunct in the summer-cold Saguenay fiord of the St. Lawrence estuary and elsewhere widely Holarctic.

Gammaracanthus ***(Pseudacanthus)***, new subgenus (Fig. 3B)
Gammaracanthus Gurjanova, 1951: 784 (*partim*)
Gammaracanthus Johnson, 1964: 78–79 (*partim*)
Gammaracanthus Barnard, 1969: 241 (*partim*)
Gammaracanthus Barnard and Barnard, 1983: 524 (*partim*)

Species content:
G. (Pseudacanthus) aestuariorum (Lomakina, 1952) (TYPE species)
G. (Pseudacanthus) ostiorum (Lomakina, 1952)
G. (Pseudacanthus) baicalensis (Sowinsky, 1915)
G. (Pseudacanthus) caspius (Sars, 1896)

Four new species, based on earlier material of "*Gammaracanthus loricatus*" and "*G. aestuariorum*," from Canadian arctic coastal marine localities, to be described (E. L. Bousfield, unpubl. data).

Diagnosis:

Body generally weakly carinate on peraeon (except *P. caspius*); lateral ridges medium to weak. Rostrum slightly deflexed, not extending beyond peduncular segment 1 of antenna 1. Inferior head lobe short, extending laterally about width of base. Antenna 1, accessory flagellum 4–5 segmented. Antenna 2, peduncle short, flagellum not longer than peduncular segment 5, 10–14 segmented.

Mandible, left lacinia irregularly 5- dentate; spine-row medium (6–10 blades). Maxilla 1, outer plate with 7–9 and/or 10–11 spine teeth.

Coxal plates generally less deep than corresponding peraeonal plates (except *P. caspius*), lateral rib not prominent. Gnathopod 1, propod closely subequal in size to that of gnathopod 2, but differing in form (expanding medially in 1); hind margin nearly straight, about equal in length to palmar margin; postero–distal angle with distal (postdepression) spine cluster and prominent long spine.

Peraeopods medium strong. Peraeopods 3 and 4, bases longer than coxal plates. Peraeopods 5 and 6 subequal, 6 slightly the longer; bases of peraeopods 5–7 increasing regularly in length posteriorly, and differing slightly in form; coxae anterolobate lobes rounding below (except *P. caspius*).

Pleon plates, hind corners acuminate, not strongly produced. Pleopod 2 weakly sexually dimorphic; inner ramus, distal 7–8 segments of each armed on outer margin with short spine (male).

Taxonomic commentary:

Members of the *aestuariorum–ostiorum* species complex are closely similar, and probably of relatively recent origin. *Pseudacanthus caspius* retains the strong carination and deeper coxal plates of the *Gammaracanthus* subgeneric group, but exhibits unique features such as plumose setae on the inner ramus of uropod 2, perhaps meriting its own subgeneric status.

Distribution:

Occurring along holarctic marine coastlines, mainly in relatively shallow brackish estuaries, lagoons, and lakes; one species occurs in Heart Lake in western Quebec, a relict lake of the former Champlain Sea basin (Dadswell 1974). *Pseudacanthus caspius* is confined to deep waters of the Caspian Sea, and *P. baicalensis* to Lake Baikal.

Relictacanthus, new genus (Fig. 3C)
Gammaracanthus Loven, 1861: 287
Gammaracanthus Sars, 1867: 73 (*partim*)
Gammaracanthus Sars, 1895: 493 (*partim*)
Gammaracanthus Gurjanova, 1951: 784 (*partim*)

Species composition:
Relictacanthus relictus (Sars, 1895) (TYPE species).
Relictacanthus lacustris (Sars, 1867).

Diagnosis:

Rostrum nearly straight, tip not (or slightly) decurved. Inferior head lobe broadly rounded, short. Antenna 1, peduncular segments elongate, segment 2 longer than 1, segment 3 nearly equal in length to segment 1. Antenna 2, peduncular segments 4 and 5 elongate, subequal; flagellum shorter than peduncular segment 5.

Mandible, palp segment 3, terminal setae short, less than half length of segment; blade row of 10–14 slender blades. Maxilla 1, outer plate with 10 tall apical spine teeth; palp with plumose outer marginal setae.

Coxal plates shallow, plate 2 distinctly shallower than 1 and 3. Gnathopods very large, markedly unequal in size and form, gnathopod 1 larger; bases lacking posterior marginal groups of "comb setae," long setae in several clusters. Gnathopod 1, carpus slender, longer than carpus of gnathopod 2; propod much the longer, broadest medially; postero-distal angle with distal (postdepression) group of spines, one very long.

Peraeopods elongate, slender; dactyls small. Peraeopod 4 distinctly longer than peraeopod 3. Peraeopods 5–7, bases narrow, markedly unequal in size, largest posteriorly; segment 5 (of peraeopods 5 and 6) elongate, nearly equal to segments 4 and 6 combined.

Pleon plates squared, little or not acuminate behind. Pleopod rami slender, subequal, those of pleopod 2 unmodified in male. Uropods 1 and 2, rami slender, subequal, nearly equal in length to respective peduncles. Uropod 3, rami narrowly paddle-shaped, length about 5× width. Telson lobes separated nearly to base, each with fine setules medially as well as laterally.

Sternal gills present mid-ventrally on peraeopon segments 2–7 and pleon 1.

Distribution:

Known only from large deep freshwater lakes of Fennoscandia and the Karalian peninsula (USSR).

Overview of Amphipod Morphology and Life Cycle

Members of family Pontporeiidae, especially within the *Pontoporeia* complex (Fig. 1), are sediment burrowers and detritivores. Males and females are strongly sexually dimorphic at maturity, very different in appearance and life style. The female (Figs. 1A–C) is a benthic burrower, with short antennae, small eyes, weak pleopods, and short, spinose uropod 3. The male is a free-swimming animal, with pelagic mating life style (Fig. 1D). Relative to the female, the male is slightly smaller; its long antennae bear numerous cup-shaped, vibration-sensory calceoli on the flagellar and distal peduncular segments, the eyes are large, and the gnathopods are differently shaped (Fig. 1E). Moreover, the distal segments of peraeopod 7 are strongly modified, presumably amplexing in function (Fig. 1F). The pleopods are larger and more powerful, uropod 3 is much larger and the rami richly armed with swimming setae (Fig. 1G), but the urosomal hump is smaller and less strongly toothed than in the female.

During the reproductive cycle, males swarm up into the water column, apparently synchronously, where they search out and mate with females that swim up later. Shortly afterwards, the nonfeeding male dies, but the female returns to the bottom. There she nourishes and broods her newly inseminated eggs which develop and hatch several months later.

Major character traits that distinguish the three genera of Pontoporeiidae considered here are provided in Fig. 2. Member species of *Monoporeia* (Fig. 1C) differ superficially from *Pontoporeia* in lacking a pronounced urosomal hump, and in having a shallow anterior lobe on coxa 5. Their life style is similar to that of *Pontoporeia* but members are restricted to holarctic marine shallows and brackish or fresh, inland seas and lakes.

The eight(+) species of *Diporeia* (Fig. 1B) differ superficially from members of the other genera in having double sternal gills and a large peraeopod 5 (basis equal to or larger than that of peraeopod 6). In the "long-horned" (*filicornis*) subgroup the male antennae are very long (flagellum 45–65 segmented) and the rami of uropod 3 are strongly setose. In the "short-horned" (*brevicornis*) subgroup, the male antennae are shorter (flagellum of 19–35 segments) and the rami of uropod 3 are relatively weakly setose.

Ecologically, species of the *filicornis* group tend to be cold-stenothermal, confined below the summer thermocline, in temperatures below 15°C, whereas *brevicornis* species are more eurythermal and may live at or above the summer thermocline, in temperatures as high as 20°C. Confirmation of these ecophenotypic trends has been noted in males of the two groups from Mazinaw Lake, Ontario, by Vainola and Varvio (1989). Although precise correlations have not been made (e.g. Dadswell 1974), *filicornis* types tend to be more common in soft-water lakes, *brevicornis* species in hardwater lakes.

Members of the eusiroidean holarctic family Gammaracanthidae (Fig. 3) are large, benthic and epibenthic, free-crawling and free-swimming carnivores that prey mainly on mysids and other small crustaceans. The animals have strongly rostrate heads and carinate bodies; the gnathopods are powerfully subchelate and raptorial; the ambulatory legs are elongate (peraeopod 6 always the longest); the pleopods are strongly developed; the rami of uropod 3 are large and paddle-shaped; and the telson short and bilobate.

Within subgenus *Gammaracanthus*, the dorsal body carinations are strongly toothed, the head process and lateral ridges are pronounced, the hind corners of pleon side plates 2 and 3 are strongly produced, but sternal gills are lacking (Fig. 3A, inset). Pleopod 2 is sexually dimorphic (Fig. 3A, inset), and gnathopod 1 is distinctly smaller than 2. The five full species and/or forms (mostly new to science) are coastal marine or polyhaline.

Members of subgenus *Pseudacanthus* also lack sternal gills, but tend to have less strongly toothed carinations (except *G. (P.) caspius* Sars): the pleon plate hind corners are acuminate, not produced (Fig. 3B). The pleopods are less strongly sexually dimorphic, and gnathopods 1 and 2 are subequal in size. The component four described species occur mainly in cold, brackish estuaries and coastal freshwater lakes or inland seas that were connected (variously in late Tertiary times) to holarctic marine waters (see Lomakina 1952; Johnson 1964; Dadswell 1974; Barnard & Barnard 1983).

The two known species of *Relictacanthus* differ from members of the genus *Gammaracanthus* in having more slender and less strongly carinated bodies, more slender peraeopods, larger gnathopod 1 (>gnathopod 2, with long palmar spine), median sternal gills on peraeon segments 2–7 and pleon 1 (Fig. 3E inset), and sexually similar pleopods (Fig. 3C, inset). These animals are confined to deep, freshwater lakes of Norway, Fennoscandia, and the northwestern USSR (Sars 1895; Barnard and Barnard 1983).

In summary, the taxonomic recognition of new generic-level entities within *Pontoporeia* appears to be generally consistent with those derived by Vainola and Varvio (1989) based on electrophoretic enzyme analyses. One might predict similar electrophoretic confirmation of the gammaracanthid taxa newly proposed herewith.

Distributional Analysis

The 11 known species of *Pontoporeia* and *Monoporeia* occur in holarctic marine and brackish waters (Fig. 4A). Members of *Pontoporeia* are coastal marine forms widely distributed throughout the holarctic, with access to deep-water refugia, and thus of slight marine-glacial relict significance. Members of *Monoporeia*, however, are dominant in cold-brackish estuaries and coastal or marine-glacial freshwater lakes throughout the holarctic region, especially in fresh waters of the Baltic trans-Karalian region and in the Caspian Sea. Significantly, however, none occur in interior continental lakes of Eurasia or North America nor in Lake Baikal. Members of Pontoporeiidae are passively dispersed via merging lake basins or downriver drift. As in the Mysidacea (Holmquist 1959; Dadswell 1974), their low benthic mobility and pelagic mating life style combine to prevent upstream migration from summer-cold lake bottoms, or arctic coastal centres of origin, against continuous lotic gradients, especially of summer-warm rivers (e.g. Angara River). Their ecological and morphological counterparts in Lake Baikal appear to be endemic species of *Micruropus*, convergent species that have a gammaroidean but not pontoporeioidean ancestry (see Bazikalova 1945; Bousfield 1977).

By contrast, the eight known species of *Diporeia* occur only in continental proglacial lakes and lake basins of North America (Fig. 4B). Most species (e.g. *D. hoyi*, *D. brevicornis*, *D. kendalli*, and some new forms of the *brevicornis* group), occur in the St. Lawrence Great Lakes basin. The *filicornis* group predominates in lakes of the Precambrian Shield; isolated populations occur also in a few Pacific coastal remnant proglacial lakes (e.g. *D. erythrophthalma* in Lake Washington).

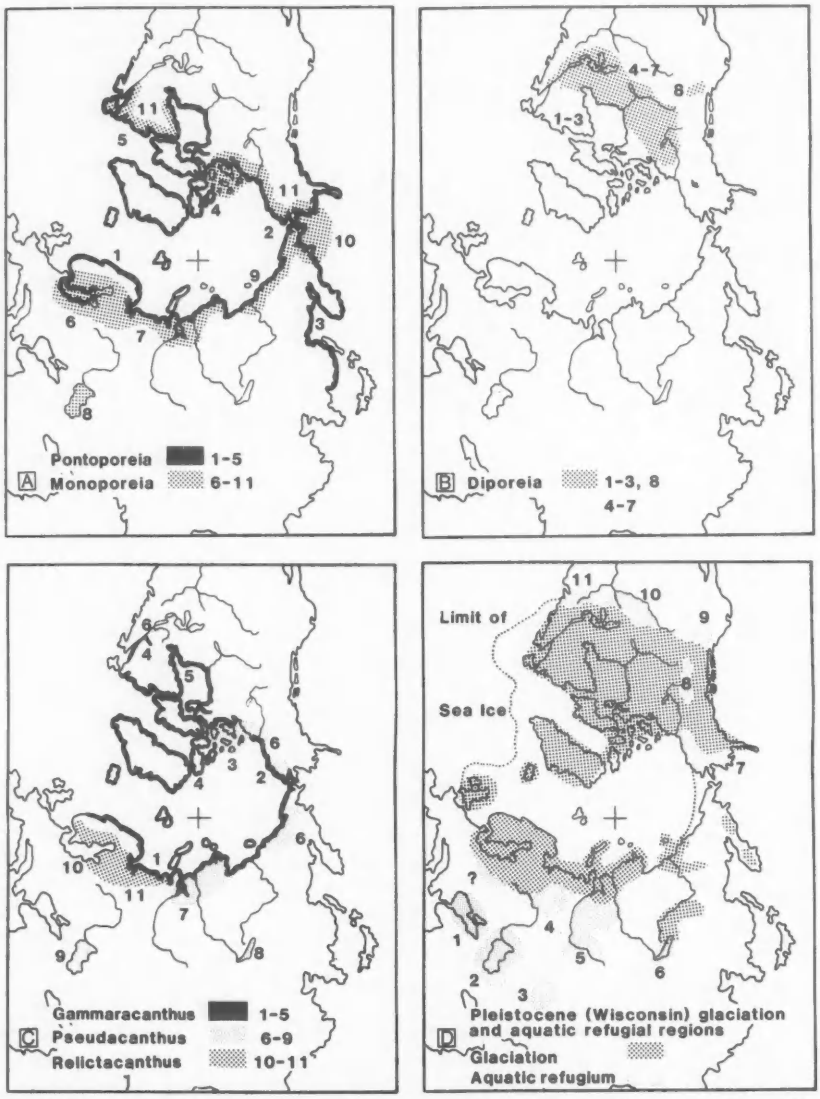

FIG. 4. Distribution of Pontoporeiidae and Gammaracanthidae relative to Pleistocene glaciation. Distributional information provided by Barnard and Barnard (1983) and earlier authors is supplemented by more recent records (e.g. E. L. Bousfield, unpubl. data). A; (1) *Pontoporeia femorata* (Kr); (2) *Pontoporeia*, new species 1; (3) *P. ekmani* (Bulych); (4) *Pontoporeia*, new species 2; (5) *Pontoporeia*, new species 3. (6) *Monoporeia affinis* (Lindstr.); (7) *Monoporeia gurjanovae (Birula); (8) Monoporeia microphthalma* (Sars); (9) *Monoporeia*, new species 1; (10) *Monoporeia*, new species 2; (11) *Monoporeia*, new species 3. B: *Diporeia*, new genus; (1–3,8) *filicornis* group; 4–7 *brevicornis* group: (1) *Diporeia hoyi* (Smith); (2) *Diporeia kendalli* (Norton); (3) *Diporeia filicornis* (Smith); (4) *Diporeia brevicornis* (Segerstrale); (5) *Diporeia intermedia* (Segerstrale); 6. (6) *Diporeia*, new species 1; (7) *Diporeia*, new species 2; (8) *Diporeia erythrophthalma* (Waldron). C: *Gammaracanthus*: (1–5) subgenus *Gammaracanthus*; (6–9) subgenus *Pseudacanthus; (10, 11) Relictacanthus*, new genus: (1) *Gammaracanthus* (G.) *loricatus* (Sabine); (2) *Gammaracanthus* (G.), new species 1; (3) *Gammaracanthus* (G.), new species 2; (4) *Gammaracanthus* (G.), new species 3; (5) *Gammaracanthus* (G.), new species 4. (6) *Gammaracanthus (Pseudacanthus) aestuariorum* (Lomakina); (7) *G. (P.) ostiorum* (Lomakina); (8) *G. (P.) baicalensis* Sowinsky; (9) *G. (P.) caspius* Sars; (10) *Relictacanthus lacustris* (Sars); (11) *Relictacanthus relictus* (Sars). D: Maximum extent of Pleistocene (Wisconsin) glaciation and aquatic refugial regions: (1–6) in Eurasia; (7–11) in North America. (1) Black; (2) Caspian; (3) Aral; (4) Karalian; (5) West Siberian (6); Baikalian; (7) Alaskan; (8) Cordilleran; (9) Western (Pacific); (10) Central (Ohioan); (11) Eastern (Atlantic).

Patterns of distribution of Gammaracanthidae (Fig. 4C) are, collectively, very similar to those of *Pontoporeia* and *Monoporeia* within the Pontoporeiidae. Important differences are: (1) *Gammaracanthus (P.) baicalensis* Sowinsky, but not *Monoporeia*, occurs in Lake Baikal. Many ancestral animal groups (including that of the Baikal seal, *Phoca sibirica*) successfully penetrated up the Angara River from the Arctic Ocean (via Lake Yenesei) to Lake Baikal. These apparently included the ancestor of *G. (P.) baicalensis*, doubtless aided by its benthic ambulatory ability and benthic mating style. (2) Some species of *Pseudacanthus* (e.g. of the *aestuariorum* group) but apparently not *Monoporeia*, occur in marine glacial lakes (e.g. Heart Lake) of the Champlain Sea bed of eastern Canada (see Dadswell 1974). Speculatively, species of *Monoporeia* may have occupied the region during the early (i.e. marine) phases of the Champlain Sea postglacial intrusion, but were replaced during the late (i.e. continental freshwater) phases by species of *Diporeia* that occur there today. (3) *Gammaracanthus* (both subgenera) is well represented in the Chukchi and Beaufort seas, but not yet recorded from the Bering Sea or North Pacific region. By contrast, the *Pontoporeia* and *Monoporeia* groups are common in the latter regions, especially along the Asiatic Pacific coast of this presumed refugial region. (4) Species of *Relictacanthus* are known only from fresh waters of the Baltic-trans-Karalian region, whereas those of regional counterpart genus *Monoporeia* occur widely elsewhere.

Extensive marine refugial regions (free of summer ice) were confined to three main areas (Fig. 4D): the Bering and southern Chukchi seas; and the European and North American Atlantic shores immediately south of the ice limits (Bousfield and Thomas 1975; Gentry and Sutcliffe 1981, figure 15.2). Marine and brackish-water crustaceans apparently spread rapidly around polar shores following postglacial coastal ice melt. A few high arctic species evidently became isolated in southern summer-cold refugia. These include the marine species, *Gammaracanthus loricatus*, in the Saguenay fiord, the oligohaline and brackish-water members of the *Pseudacanthus aestuariorum* group in Heart Lake, and new species of *Monoporeia* along summer-cold shores of the St. Lawrence estuary. On the Pacific coast, a subspecies of the *Pontoporeia femorata* group occurs in fiords of the coast of Southeastern Alaska and British Columbia (see Dadswell 1974; Bousfield, unpubl. data).

The extent of freshwater refugial regions, primarily ice-dammed lakes in unglaciated continental regions, was more widespread than that of the marine refugia. The Eurasian refugia encompassed at least six main glacial relict lake basins: the Black, Caspian, Aral, Karalian (Upper Volga), West Siberian (Pur-Mensi-Yenisei), Baikalian, and possibly others in the upper Lena, and what is now the Upper Dnieper and Polish Lakes region (Fig. 4D, partly after Segestrale 1982; Hughes et al. 1977). These were all at relatively low altitudes (1–300 m a.s.l.), intermittently interconnected, but only in latest stages accessible from the sea. The North American refugia included the Alaskan, Cordilleran, Western (Pacific), Ohioan (Central), and Eastern (Atlantic) proglacial lake systems (after McAllister 1961; Dadswell 1974). Most lakes were at relatively high altitudes (some >500 m a.s.l.) with greater isolation from each other and from the sea, especially in the central region. Noteworthy is the complete isolation of continental glacial relict lake refugia of Eurasia from those of North America.

Freshwater amphipods endemic to Eurasia (e.g. *Pallasea*, according to Segerstrale 1982; *Relictacanthus*, this study) and those endemic to North America (e.g. *Diporeia*, this study) are apparently intolerant of salt water and were thus "locked into" their original proglacial basins and subsequent glacial relict lake systems. They did not spread via brackish waters to adjacent regions, as maintained by Dadswell (1974) and others. The degree of euryhalinity that they observed in presumed single "species" such as *Pontoporeia "affinis"* and "*Gammaracanthus loricatus*" can now be attributed mainly to uncritical taxonomy. Each of those names actually contained complexes of both brackish-water and primary freshwater species.

The Alaskan lacustrine refugium apparently existed in isolation as well. Although accessible to brackish-water relicts, it provided no pathway for postglacial interchange of Palaearctic and Nearctic primary freshwater relicts. Moreover, the modern lakes of all refugial basins are characteristically deep, the hypolimnion in summer is cold (<10°C), and the surface in winter is ice-covered. These physical features tend to prevent further postglacial dispersal of the endemic glacial-relict faunas.

Dadswell's contention that the entire Holarctic distributional pattern of relict organisms can be explained in terms of the last (Wisconsin) glaciation is reasonably firmly based, but not in the sense he envisaged. Thus, from taxonomical, physiological, and distributional–ecological aspects, diversity within both the Pontoporeiidae and Gammaracanthidae is here demonstrated to be very much higher than he recognized, and more in agreement with the degree of diversity and antiquity discovered by Vainola and Varvio (1989) on a genetic basis. The earlier thesis of "rapid evolution" from marine ancestors during the relatively brief period of late Pleistocene glaciation and recent times (e.g. of Segerstrale 1982) does not rationally explain the existence of so many modern species and generic and subgeneric groupings within these families, nor does it account for their modern ecologically and biogeographically discrete (disjunct) distributions detailed here (Fig. 4).

Alternative Scenarios

If the origin and evolution of these cold-stenothermal crustacean groups cannot be derived rationally within a Pleistocene time frame, what other (earlier) scenarios might be proposed? What is a more credible paleohistorical timing of a presumed common marine ancestor to present-day members within the Pontoporeiidae, on the other hand, and the Gammaracanthidae on the other?

In a phyletic sense, both these groups are considered to be relatively ancient (see Bousfield 1982b, 1984). Thus, with respect to *Diporeia*, a prolonged evolutionary period is presumably required for development of its distinctive generic level morphology and its *filicornis* and *brevicornis* subgroupings. Furthermore, the endemicity of pontoporeiid groups within high interior lakes of North America, despite the passive and very limited dispersal capabilities of component species, would indicate continental penetration by marine ancestors when sea levels were much higher, and the interior was at least partly marine-inundated. Such conditions were met during the late Cretaceous, about 80 million years B.P. (see Howarth 1981, figure 13.19). Subsequently, as in the Eocene, some 50 million years B.P.), seas were low and continents high (Adams 1981, figure 14.4D). In Eurasia at the latter time, however, the continent was inundated ("split") by the Obik Sea that connected the Arctic Ocean with the warm epicontinental Tethys Sea. This connection was not closed until the Oligocene Epoch, 30 million years B.P. (Adams 1981, figure 14.4D). However, marine

climates at that time may have been too warm for these presumed cold-stenothermal ancestral amphipod crustaceans.

Alternatively, if early Tertiary scenarios do not provide a totally adequate explanation, we might examine the situation during the Pliocene Epoch, about 3 million years B.P. (Adams 1981, figure 14.8). Cooling marine conditions at that time might have been suitable for southward penetration of continental freshwaters by both family groups. However, the time frame for present genetic diversity within the Pontoporeiidae (and perhaps also the Gammaracanthidae) would have been too brief, according to the conclusions of Vainola and Varvio (1989). Answers to the "time frame problem" of amphipod diversity in this instance await a more refined application of their methodology, the karyology methodology of Salemaa (1986), or the DNA–DNA hybridization methodology, pioneered so effectively in avian phylogeny by Sibley and Ahlquist (1983).

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Effect of Nitrite on the Embryonic Development of Atlantic Salmon (*Salmo salar*)

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Williams, E. M., and F. B. Eddy. 1989. Effect of nitrite on the embryonic development of Atlantic salmon (*Salmo salar*). 1989. Can. J. Fish. Aquat. Sci. 46: 1726–1729.

Effects of nitrite on eggs, alevins, and fry of Atlantic salmon (*Salmo salar*) were studied and of these developmental stages eggs were the most resistant with a 24-h LC_{50} value of 3276 mg·L^{-1} N·NO_2. Upon hatching tolerance sharply decreased, the 24-h LC_{50} value for early alevins (2940 mg·L^{-1} N·NO_2) decreasing to 121.8 mg·L^{-1} N·NO_2. Development in freshwater or dilute saline (10 mmol·L^{-1} NaCl) proceeded normally without mortalities. Long-term exposure to nitrite concentrations as low as 14 mg·L^{-1} N·NO_2 delayed hatching and retarded embryo growth and development as well as producing cardiovascular effects such as a reduced heart rate. The physiological and environmental implications of nitrite exposure are discussed.

Les auteurs ont étudié les effets du nitrite sur les oeufs, les alevins vésiculés et les alevins du saumon de l'Atlantique (*Salmo salar*) et ils ont constaté que, parmi ces stades de développement, les oeufs étaient les plus résistants, la valeur de la CL_{50} en 24-h étant de 3276 mg·L^{-1} de N·NO_2 pour ces derniers. À l'éclosion, il y a eu une diminution marquée de la tolérance, la valeur de la CL_{50} en 24-h pour les alevins vésiculés précoces (2940 mg·L^{-1} de N·NO_2) passant à 121,8 mg·L^{-1} de N·NO_2. Le développement dans l'eau douce ou dans une solution saline diluée (10 mmol·L^{-1} de NaCl) s'est fait normalement sans qu'il y ait de mortalité. Une exposition de longue durée à des concentrations de nitrites aussi faibles que 14 mg·L^{-1} de N·NO_2 a retardé l'éclosion et la croissance des embryons tout en ayant des effets sur le système cardio-vasculaire, comme un rythme cardiaque réduit. Une discussion suit sur les incidences physiologiques et environnementales de l'exposition aux nitrites.

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Nitrite in natural aquatic systems varies in concentration according to temperature and oxygen availability with anoxic regions having the highest concentration (see review Eddy and Williams 1987). Some inshore sites which contain rotting vegetation and algae can have nitrite concentrations as high as 13 mmol·L^{-1} (180 mg·L^{-1} N·NO_2) (McCoy 1972). However, most freshwaters even when polluted by organic matter contain lower nitrite levels (Eddy and Williams 1987). Fish embryos found in regions experiencing episodes of nitrite exposure would be at a disadvantage since unlike adult fish they would be unable to escape to areas of normoxic water.

In recent years many freshwater systems including salmonid rivers (EIFAC 1984) have experienced increased nitrogenous input resulting in elevated levels of nitrite, nitrate, and ammonia. Use of such water for salmonid hatcheries may be dictated by a growing scarcity of convenient good quality freshwater supplies, while nitrogenous contamination of existing hatchery water supplies is always a possibility. Thus it is important to recognize the physiological effects of nitrite poisoning in salmonid eggs and alevins.

Most studies have found that fish eggs and yolk sac fry are more tolerant to nitrite than adults (Russo et al. 1974; Perrone and Meade 1977; Thurston et al. 1978; Palachek and Tomasso 1984; Hasen and MacIntosh 1986). The toxicity of nitrite to marine red drum larvae (*Sciaenops ocellatus*) was studied by Holt and Arnold (1983), who reported 91% survival when exposed to 36 mmol·L^{-1} nitrite (504 mg·L^{-1} N·NO_2) for 48 h with only 25% surviving exposure to 0.7 mmol·L^{-1} (9.8 mg·L^{-1} N·NO_2) for 14 d. Brownell (1980) studied nitrite tolerance in five species of marine fish larvae finding that 24-h LC_{50} values ranged from 88 to 174 mmol·L^{-1} (1230–2440 mg·L^{-1} N·NO_2) while first feeding was inhibited by 50% in larvae exposed to nitrite in the range of 24–32 mmol·L^{-1} (330–450 mg·L^{-1} N·NO_2). Thus in laboratory studies some marine fish larvae are very tolerant to nitrite when compared with adults, but it is unlikely that such high nitrite concentrations would occur naturally although moderately high levels can occur in recirculating freshwater systems (Collins et al. 1975).

The aim of this study was to determine some sublethal effects of nitrite on the development of Atlantic salmon (*Salmo salar*) eggs and yolk sac fry using weight gain, hatching time, and heart rate as indicators of physiological integrity. Such observations may be of use in salmonid rivers and hatcheries receiving water with a significant nitrogenous input.

Methods and Materials

Atlantic salmon eggs and alevins (yolk sac fry) were obtained from the Salmon Rearing Unit of the Freshwater Fisheries Laboratory, Almondbank, Scotland.

In this study the developmental stages of the salmon embryo are described according to the system of Pelluet (1940). Stages 8–12 cover development from the first appearance of "eyed" embryos to the period of hatching, while stages 13–15 refer to alevins (yolk sac fry) and stage 16 refers to fry where the yolk sac has completely disappeared and first feeding commences.

In late November freshly stripped, unfertilized eggs together with milt were transferred to the Dundee aquarium where the eggs were fertilized. The eggs were held in the dark in running water of average temperature 5°C (Range 3–8°C), pH 6.8–7.0 with an ionic content in millimoles per litre, sodium, 0.22; calcium, 0.1, and chloride, 0.2 for 10 wk until development stage 8 (Pelluet 1940) when eyes, heart, and circulatory system were clearly visible. Upon hatching (15 wk after fertilization) alevins were transferred to tanks containing 1 L of aerated water, temperature 5–9°C, which was changed weekly. Prior to stage 8 experiments were not performed since the eggs were intolerant of handling and it was difficult to assess sublethal effects of nitrite in early and undeveloped embryos. A population of stage 8 eggs from the main group was exposed for a period up to 10 wk (from February onwards) to a nominal series of nitrite concentrations 0, 0.1, 1, 10, and 100 mmol·L^{-1} (0, 1.4, 14, 140, and 1400 mg·L^{-1} N·NO_2). For each treatment vessels containing 10–14 eggs or alevins in 150 mL of water (ion content and pH as described above) were placed in a shallow water bath maintained at 5–9°C. The required nitrite concentrations were obtained by volumetric dilution of a 1 M sodium nitrite solution. These nitrite incubation media were changed weekly and the virtual absence of nitrifying and denitrifying bacteria in the experimental system ensured stable nitrite levels. Analysis of the media by the method of Shechter et al. (1972) showed that measured nitrite levels were always within ± 10% of the nominal value. A further group of eggs was kept in 10 mmol·L^{-1} sodium chloride and the medium was changed as before.

Once a week for 10 wk the eggs or alevins were removed and placed individually on a glass microscope slide in 0.5 mL of cold water and quickly examined under a binocular microscope (× 10). Growth, development, and heart rate (time taken for 100 beats) were noted together with any mortalities. To establish weight gain, all the animals from a vessel were removed, gently blotted dry and weighed. Since the alevins were more delicate they were removed and carefully blotted dry before transfer to a preweighed vessel containing cool water. It had been previously established that sibling eggs were of uniform weight, such that individual weight could be calculated from the combined weight.

Tests to determine the acute toxicity of nitrite to eggs and alevins was carried out in 3-L tanks and the 24 h median lethal concentration (LC_{50}) was calculated (Parrish 1985). For each developmental stage tested an average of 214 ± 24 animals were used per test with three to four tests being performed for each LC_{50} determination. A plot of percentage mortality against water nitrite concentration was used to determine the water nitrite concentration at which 50% mortality occurred.

Results

Exposure of Eggs and Alevins to Nitrite

No mortalities occurred in eggs (stage 8–12) exposed to a maximum of 10 mmol·L^{-1} nitrite over a 4-wk period, though exposure to 100 mmol·L^{-1} prevented hatching with 100% mortalities occurring within 4 wk (Table 1). Both eggs and alevins exposed to 10 mmol·L^{-1} nitrite showed 50% mortality in 9 wk and 100% mortality in 10 wk while exposure to 1 mmol·L^{-1} produced 50% mortality in 10 wk and 100% in 12 wk. Alevins exposed to 0.1 mmol·L^{-1} nitrite died 2 wk after hatching, from unknown causes while the unexposed group suffered 33% mortality over the 11-wk experimental period probably caused principally by handling. Eggs kept in 10 mmol·L^{-1} sodium chloride showed no mortalities and hatched normally (Table 1) as did the main population of sibling eggs.

TABLE 1. Toxicity of nitrite in developing Atlantic salmon embryos. The developmental stage of the embryo salmon was described according to Pelluet (1940). The mean animal weight is shown. Age, months since fertilization.

		Long term toxicity	
Developmental stage	Embryo weight (g)	Nitrite concentration mmol·L^{-1} (mg·L^{-1} N·NO_2)	50% Mortality (wk)
Eggs (Stage 8–12)	0.147	100 (1400)	4
		10 (140)	9
		1 (14)	10
		Short term toxicity	
		24-h LC_{50}	Age (m)
Eggs (Stage 11–12)	0.147	235 (3290)	4–5
Alevins (Stage 13)	0.17	210 (2940)	5
Alevins (Stage 15–16)	0.17	8.7 (121.8)	6–7
First-feeding fry	1.04	0.74 (10.4)	7
3-mo old fry		0.73 (10.2)	10
Parr* 10–25		0.72 (10.1)	12–24

*Data from Eddy et al. 1983.

Acute Exposure (24-h LC_{50} Toxicity Tests)

The 24-h LC_{50} value for stage 11–12 eggs was 235 mmol·L^{-1} (2390 mg·L^{-1} N·NO_2), which fell immediately upon hatching to 210 mmol·L^{-1} (2940 mg·L^{-1} N·NO_2) (Table 1). Stage 15 alevins were more susceptible to nitrite showing a 24-h LC_{50} value of 8.7 mmol·L^{-1} (122 mg·L^{-1} N·NO_2) while the value for first feeding fry decreased to 0.74 mmol·L^{-1} (10.4 mg·L^{-1} N·NO_2), about the same as that for 3-mo old fry, with a 24-h LC_{50} value of 0.73 mmol·L^{-1} (10.2 mg·L^{-1} N·NO_2) (Table 1). Thus there was a marked increase in nitrite toxicity as the development stages progressed from eggs to alevins and then to fry.

Hatching and Egg Weight

After 4 wk in all nitrite containing media egg weight was around 147 mg·egg^{-1} with a similar value for unexposed eggs (stages 8–12). Just before hatching there was an increase in weight associated with the highest nitrite levels (Fig. 1), which also delayed hatching the longest (Fig. 2). Upon hatching loss of the chorion and the perivitelline fluid resulted in a large weight decrease followed in unexposed alevins by a rapid weight gain (66–138 mg per individual in 4.5 wk or about 14 mg·wk^{-1}). Nitrite exposure delayed this weight gain by 2–3 wk (Fig. 1).

Heart Rate

In stages 8–12 heart rate increased from 72 to 138 beats·min^{-1} in unexposed eggs and from 72 to 115 beats·min^{-1} in nitrite exposed groups, and in each case the rate was greatest 1–2 wk post hatching (Fig. 3). Immediately upon hatching heart rate increased significantly in all groups from 94.6 to 104.9 beats·min^{-1} ($p<0.05$), the increase being independent of nitrite levels. Eggs exposed to 100 mmol·L^{-1} nitrite showed a sudden decrease in heart rate after 4 wk the rate decreasing from 77 to

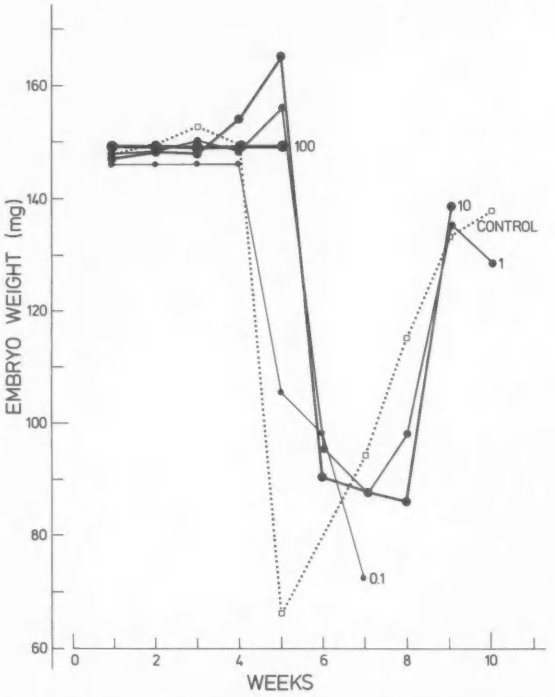

FIG. 1. Effect of long-term nitrite exposure on weight gain in Atlantic salmon eggs and alevins. Each point is the mean weight (see text for details). Nitrite concentrations in millimoles per litre (see method for details). Hatching occurred between week 4 and 6; eggs at 100 mmol·L^{-1} all died before hatching.

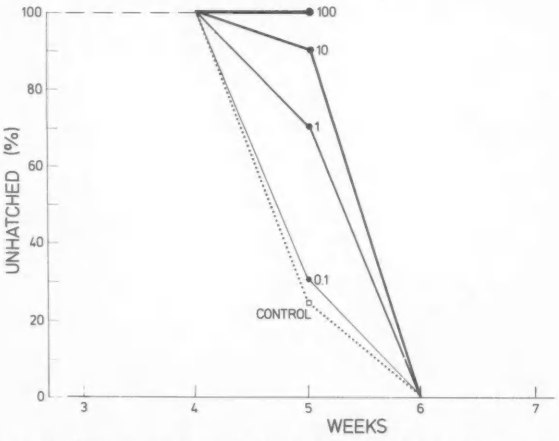

FIG. 2. Effect of long-term nitrite exposure on hatching (weeks 4–6) in Atlantic salmon eggs. Symbols as in Fig. 1.

less than 65 beats·min^{-1}, a phenomenon also noted in eggs exposed to 10 mmol·L^{-1} nitrite at 9 wk (Fig. 3). Observations of the embryos revealed irregular heart beats with periods of several seconds when no contractions occurred.

Development

The blood of embryos exposed to 100 mmol·L^{-1} nitrite for 3–4 wk was a brown colour, characteristic of methaemoglobin

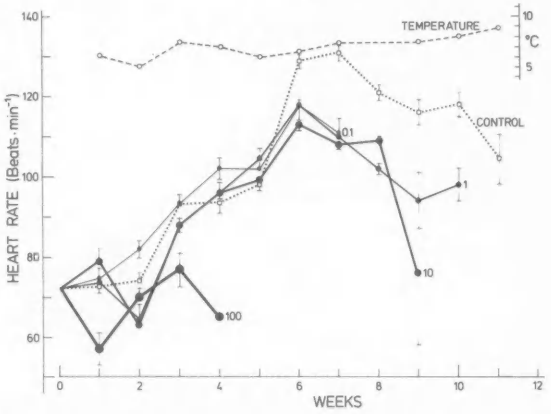

FIG. 3. Changes in Atlantic salmon embryo heart rate during long-term nitrite exposure. Ambient water temperature is also shown. Means ± SE mean are shown but for clarity some error bars have been omitted. Symbols as in Fig. 1.

and also there was evidence of hypovolaemia and arhythmic heart beat, and this group died before hatching. Stage 8 and 9 eggs exposed to nitrite levels exceeding 1 mmol·L^{-1} exhibited retarded gill development while stage 13 yolk sac fry exposed for 5–6 wk showed evidence of methaemoglobinaemia, especially noticeable in alevins exposed to 10 mmol·L^{-1} nitrite. These alevins compared with the normal group were inactive, rested on the tank bottom and exhibited pronounced opercular movements a symptom of nitrite poisoning in adult fish (Margiocco et al. 1983; Watenpaugh and Beitinger 1985). Other striking features resulting from nitrite exposure were underutilized yolk sacs, bulbous heads, underdeveloped fins, and damaged vasculature.

Discussion

Whilst the chorion (zona radiata) is intact prior to hatching, salmonid eggs are relatively resistant to toxins when compared with alevins, fry, and adults. Thus eggs exposed to 10 mmol·L^{-1} nitrite for many weeks maintained normal heart rate while fry and 1-yr old parr were highly susceptible with a 24-h LC_{50} value of around 0.7 mmol·L^{-1} (Table 1; Eddy et al. 1983). Resistance of eggs to other toxins such as acid waters and heavy metals have previously been noted (Daye and Garside 1977; Eddy and Talbot 1985; Peterson et al. 1980; Brown and Lynam 1981). Susceptibility of later stages to nitrite is probably due to a decreasing contribution to the total surface area by the relatively impermeable vitelline membrane and increasing gill surface areas associated with development of respiratory and ionic regulatory function as was suggested by salmonid fry which exhibited decreased tolerance to sea water compared with earlier stages (Parry 1960; Talbot et al. 1982).

The chorion and perivitelline fluid offer protection from toxins to the encapsulated embryo although mechanisms are as yet not well understood. The chorion apparently acts as a semi-permeable membrane allowing the exchange of small ions and molecules but not larger particles such as proteins (Potts and Rudy 1969; Groot and Alderdice 1985). However the pervitelline fluid which is rich in negatively charged sialic acid residues (Kitajima et al. 1986) is negatively charged in respect to the external media of low ionic content and should theoretically

exclude chorion permeable anions such as nitrite, unless a Donnan like equilibrium exists but further work is required in this area. Development and hatching was normal in the control groups, the first in relatively soft aquarium water (NaCl <0.25 mmol·L^{-1}, about 12 mg·L^{-1} NaCl) and the second in 10 mmol·L^{-1} sodium chloride (about 585 mg·L^{-1} NaCl, approximately 2% sea water). It was noted that salmon eggs developed and hatched normally in 12.5% sea water and also in estuaries where the salinity was at about this level (Eddy 1968; Saunders 1966).

Nitrite exposure delayed hatching in a dose dependent way, the greatest delay being at the higher concentrations. Hatching is initiated by the secretion of a proteolytic enzyme (chorionase) from the epidermal gland cells (Hagenmaier 1974) resulting, together with activity of the embryo, in rupture of the chorion. Thus nitrite may interrupt synthesis, distribution or activity of the chorionase, which with inactivity of the embryo itself may delay hatching. However, nitrite exposure had no effect on an increase in heart rate noted during hatching (Fig. 3), suggesting that this aspect of cardiovascular regulation remained uninhibited.

The dose dependent swelling of eggs just prior to hatching (11% in 10 mmol·L^{-1} NO_2, Fig. 1) is of unknown origin but may reflect an increased sensitivity to osmotic stress.

After hatching normal alevins immediately began to gain weight, a process delayed for several days by nitrite exposure (Fig. 1). This may have been caused by methaemoglobinaemia with consequent inadequate oxygen supply to the tissue, and also a possible cause of developmental abnormalities. At this stage heart rate continued to increase in normal alevins but showed little further increase in exposed individuals (Fig. 3), similar to the decrease noted in heart rate in herring larvae exposed to hypotonic saline (Holliday and Blaxter 1960). In most of their normal environments salmonid fish are unlikely to experience levels of nitrite which may be toxic. However, some salmonid rivers are adjacent to areas of agricultural activity which may cause increased nitrogen input to the aquatic environment (EIFAC 1984), and it is possible that in some environments especially where water flow is slow and minimal (possibly salmon redds) elevated nitrite levels may occur. Also salmonid hatcheries relying upon nitrogen contaminated waters could experience elevated nitrite levels if nitrifying bacteria were present and if water flow were suboptimal. In such conditions it is important to be aware of the toxicological effects of nitrite.

Acknowledgments

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Specificity of the Gustatory Chemoreceptors for CO_2 and H^+ in Rainbow Trout (*Oncorhynchus mykiss*)

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Yamashita, S., R. E. Evans, and T. J. Hara. 1989. Specificity of the gustatory chemoreceptors for CO_2 and H^+ in rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. 46: 1730–1734.

Response characteristics of the gustatory chemoreceptors to CO_2 and H^+ were electrophysiologically studied in rainbow trout (*Oncorhynchus mykiss*) in decarbonated, natural water. The integrated responses of the whole nerve bundle as well as single fibre responses were recorded from the palatine nerve (a branch of VIIth cranial nerve) innervating the anterior palate and inside the upper lip. Gustatory receptors were highly sensitive to both CO_2 and H^+, with estimated threshold concentrations of 4×10^{-5} and 5×10^{-5} mol·L^{-1}, respectively. Responses to CO_2 were not affected by pH, and adaptation to amino acids and bile salts had little effect on CO_2 responses. None of the single fibers responding to CO_2 responded to other gustatory stimuli including amino acids and bile salts. We conclude that rainbow trout distinguish CO_2 from H^+, and further that chemoreceptors for CO_2 are distinct from those which detect other gustatory stimuli.

On a étudié l'électrophysiologie des chémorécepteurs gustatifs du CO_2 et du H^+ chez la truite arc-en-ciel (*Oncorhynchus mykiss*) dans de l'eau naturelle décarbonatée. On a enregistré la réponse intégrée de l'ensemble du faisceau nerveux ainsi que celle d'une fibre unique à partir d'un nerf palatin (ramification du VII[e] nerf cranien) qui innerve la partie antérieure du palais et l'intérieur de la lèvre supérieure. On a constaté que les récepteurs gustatifs sont très sensibles au CO_2 et au H^+. On estime que les concentrations liminaires sont respectivement de 4×10^{-5} et 5×10^{-5} mol·L^{-1}. Le pH n'influe pas sur la réponse au CO_2 et l'adaptation aux acides aminés et aux sels biliaires n'a que peu d'effet. Aucune des fibres réagissant au CO_2 n'ont réagi à d'autres stimuli gustatifs, y compris les acides aminés et les sels biliaires. Nous concluons que la truite arc-en-ciel peut faire la distinction entre le CO_2 et le H^+ et que les chémorécepteurs du CO_2 sont différents de ceux qui détectent d'autres stimuli gustatifs.

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Studies on fish reactions to acid and carbon dioxide gradients have attracted the attention of investigators since Shelford and Allee (1913) first described avoidance responses of several freshwater species to carbon dioxide solutions using a two-choice trough. Evidence suggests that fish orient negatively to localized increases in hydrogen ion (H^+) concentration and that pH (or a change in pH) is a major directive factor in the distribution of fishes (Shelford and Allee 1913, 1914; Jones 1947, 1948; Ishio 1960; Bishai 1962). However, as noted by Höglund (1961), the effects of acid are often confounded with those of CO_2, which is released when acid is added to water containing carbonate salts. Höglund (1961), using a fluviarium, found that the main directive factor in combined pH/CO_2 gradients is CO_2, particularly within the pH range of 7.4 to 5.5. Recently, Jones et al. (1985), monitoring preference and avoidance responses of Arctic char *Salvelinus alpinus* to plumes of H^+ and CO_2 in decarbonated water, demonstrated that fish behaviorally discriminate between H^+ and CO_2, relying principally on the latter for orientation within H^+ and CO_2 gradients. However, fish can use H^+ alone to avoid lethal levels of pH. Thus, fish appear to have two means of avoiding acidified waters: a highly sensitive, negative reaction to CO_2 and a supplementary negative response to H^+. In support of this idea, we note that the fish gustatory system is highly sensitive to CO_2 (Konishi et al. 1969; Sutterlin and Sutterlin 1970; Yamashita and Yoshii 1977) and capable of distinguishing CO_2 from H^+ (Hidaka 1970; Yoshii et al. 1980).

The objective of the present study was to determine electrophysiologically whether the rainbow trout (*Oncorhynchus mykiss*) gustatory receptors respond to CO_2 independently of H^+. The response characteristics were further examined by using cross-adaptation and single-fiber recording techniques to identify receptors (or fibers) specifically responding to CO_2. In the experiments reported here, decarbonated, natural water was used throughout to eliminate acid–CO_2 complications which confounded previous studies (Höglund 1961; Yoshii et al. 1980).

Material and Methods

Rainbow trout, 25–35 cm in body length, were obtained from the Rockwood Hatchery, Freshwater Institute, and held in fiber-

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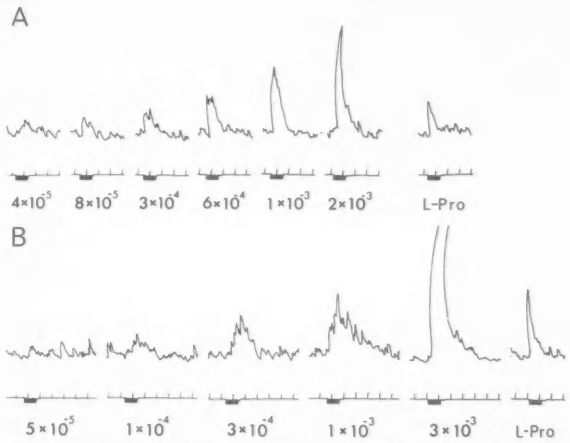

FIG. 1. Tracings of typical integrated gustatory responses to CO_2 (A) and HCl (B), recorded from the rainbow trout palatine nerve bundles. The standard responses to 10^{-3} mol·L^{-1} *L*-proline are at the far right of each column. Solid bars under each record represent stimulus duration of 5 s. Concentrations are shown in moles per litre. Time scale, each division = 5 s.

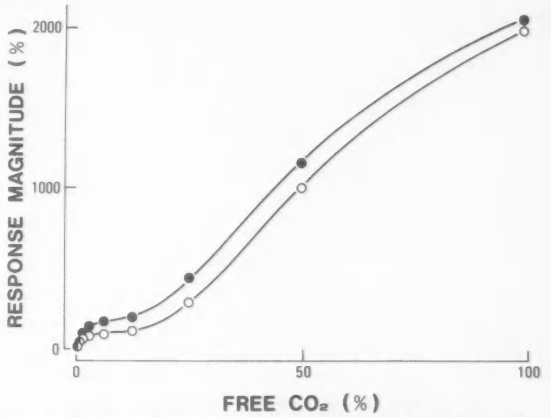

FIG. 2. Concentration–response relationships to free CO_2 in phosphate-buffered (pH = 5.0; closed circles) and nonbuffered (pH = 5.50–4.15; open circles) water. Average response magnitude is represented as a percentage of that induced by the standard stimulant, 10^{-3} mol·L^{-1} *L*-proline. CO_2 concentration is expressed as percent of saturation.

glass tanks supplied with flowing, aerated, dechlorinated Winnipeg city water (11.5–12.5°C). The water contained the following major ion concentrations: 0.51 mmol Ca^{2+}·L^{-1}, 0.24 mmol Mg^{2+}·L^{-1}, 0.14 mmol Cl^-·L^{-1}, 0.08 mmol Na^+·L^{-1}, and 0.04 mmol K^+·L^{-1}. Water hardness was equivalent to 0.78 mmol $CaCO_3$·L^{-1} (78 mg·L^{-1}). The average pH of the water was 7.7 (7.64–7.80). Dissolved inorganic carbon measured by gas chromatography (Stainton et al. 1974) was 1.43 mmol·L^{-1}. Fish were acclimated to laboratory conditions for a minimum of 6 wk prior to the experiments.

Gustatory responses were recorded from palatine nerves (VIIth cranial nerve) innervating palatal taste buds and inside the upper lip, using essentially the method described by Marui et al. (1983). Briefly, fish were paralyzed by an intramuscular injection of Flaxedil (gallamine triethiodide, 5 mg·kg^{-1} body weight), and secured in a plexiglass trough with dechlorinated water perfusing the gills throughout the experiments. After removing the eyeball, the palatine nerve bundle running through the bottom of the eyesocket was cut off centrally and its peripheral end was hooked on bipolar Ag–AgCl electrodes. Mineral oil was added to the orbit to prevent drying of the nerve preparation during recording. For single-fiber recording, the peripheral end of the nerve bundle was placed on bipolar recording electrodes and teased out with fine forceps until one or two fibers were left intact.

The neural activity of the whole nerve bundle was amplified (Grass 7P511), integrated through an integrator circuit (designed and built by Dr. S. Harada, Kagoshima University; time constant, 0.5 s), and recorded on a pen recorder (Grass 7B polygraph). The response magnitude was measured as the height of integrated responses over the stimulus duration of 5 s, and expressed as a percentage of a response to a standard stimulus, 10^{-3} mol·L^{-1} *L*-proline. Single-fiber activity was similarly amplified and stored on a magnetic tape (TEAC R-70A data recorder) for analysis. Each stimulant was tested three times consecutively with a standard time interval of 2 min, and the mean responses were obtained. For delivering chemical stimuli, the apparatus previously described was used (Marui et al. 1983; Evans and Hara 1985). A constant volume (1.8 mL) of an aqueous solution of each stimulant was drawn into a disposable pipette and injected, via an electronic time switch (Hara et al. 1973), into the stream of water perfusing (10 mL·min^{-1}) the palatal chemoreceptors. Constant temperature of stimulant was maintained by placing the pipette into a water jacket. Dye tests indicated that solutions reaching the palatal surface were not less than 50% the concentrations used. No correction was made for dilution. Stock solutions of stimulant chemicals were made with distilled water and the final test solutions were freshly prepared just before each application with the same water used to perfuse the gills and palate. For cross-adaptation experiments, the gustatory organ was perfused continuously with 10^{-3} mol·L^{-1} *L*-proline or 10^{-8} mol·L^{-1} taurolithocholic acid (adapting stimuli), and concentration series of CO_2 (test stimuli), each dissolved in respective adapting stimulant solutions, were tested. Response magnitudes were then compared with those before adaptation. The tactile stimulation was given by lightly stroking receptive areas using a fine brush or glass probe.

All experiments, unless otherwise indicated, were carried out using decarbonated water, free of excess CO_2. This was obtained from an acidification–decarbonation system, in which the CO_2 produced by addition of H_2SO_4 was removed via an air stripping procedure (Brown et al. 1984). Carbon dioxide in incoming laboratory water measured 100 ± 0.2 μmol·L^{-1}, while product water contained 49 ± 4.5 μmol·L^{-1} (approximately two times the normal atmospheric saturation). A stock solution of CO_2-saturated water was prepared by bubbling CO_2 gas into decarbonated water for 10 min. Test solutions of CO_2 and HCl, reagent grade, were prepared with decarbonated water as diluent. For CO_2 experiments, the pH of all solutions was adjusted to 5.0 with 0.1 mol·L^{-1} phosphate buffer, at which nearly all carbonates exist as CO_2 gas (Yoshii et al. 1980). The concentration of CO_2 was determined by the total dissolved inorganic carbon measured by gas chromatography (Stainton et al. 1974).

Results

The integrated responses to CO_2 solutions recorded from a whole nerve bundle were fast-adapting and phasic, and returned

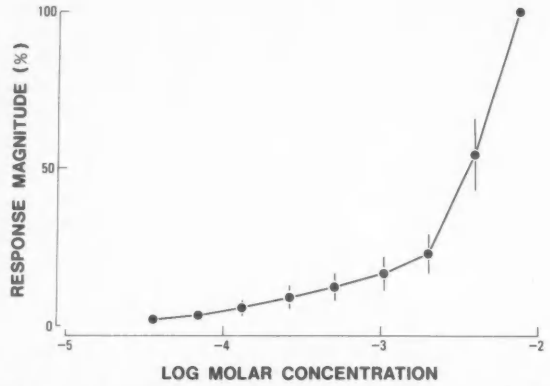

FIG. 3. Semi-logarithmic plot of the concentration–response relationship to CO_2. Average response magnitude is represented as a percentage of that induced by 10^{-2} mol·L^{-1} CO_2.

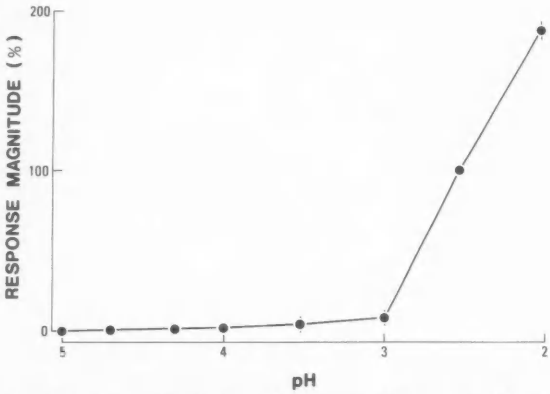

FIG. 4. Semi-logarithmic plot of the concentration–response relationship to HCl. Average response magnitude is represented as a percentage of that induced by 3×10^{-3} mol·L^{-1} HCl.

rapidly to the baseline even with continuous stimulation (Fig. 1A). The response magnitude increased step-wise with the increase in CO_2 concentration, creating a shoulder in the concentration–response curve (Fig. 2). At a concentration of 50% dilution, CO_2 evoked a response approximately 10 times that of the standard 10^{-3} mol·L^{-1} *L*-proline. The pH of CO_2 test solutions in decarbonated water ranged from 4.15 (saturated) to 5.50 (1.5%). To eliminate possible pH effects on the above CO_2 responses, the gustatory organ was perfused continuously with phosphate-buffered, decarbonated water (pH 5.0), and the same concentration series of CO_2 (phosphate-buffered, pH 5.0) was tested in the same manner (Fig. 2). The response magnitudes were slightly greater than those obtained with pH-unadjusted water at all concentrations tested, however differences were not significant. To determine a threshold concentration, amounts of CO_2 in each test solution were measured and the response magnitudes were semilogarithmically plotted (Fig. 3). The lowest CO_2 concentration required to induce an appreciable response was estimated at 4×10^{-5} mol·L^{-1}.

Integrated responses to HCl were phasic, like those to CO_2, but generally of longer duration. At the lower concentrations tested, responses were sustained 10–15 s after rinsing (Fig. 1B). HCl solutions induced a small but clear response at 5×10^{-5} mol·L^{-1} (pH 4.4) that slowly built up until the H^+ concentration reached 10^{-3} mol·L^{-1} (pH 3.0). The response magnitude increased sharply with further increase in the H^+ concentration (Fig. 4).

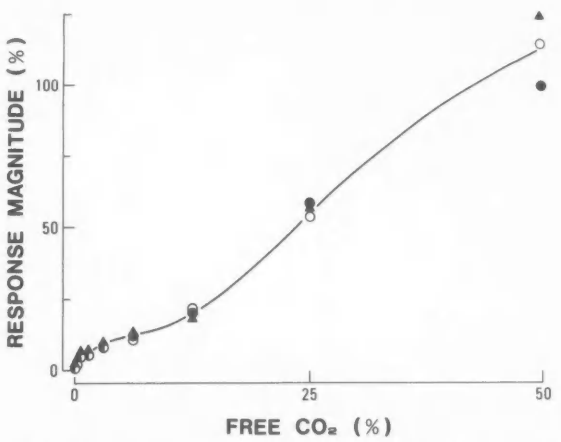

FIG. 5. Effects of adaptation to 10^{-3} mol·L^{-1} *L*-proline (open circles) and 10^{-8} mol·L^{-1} taurolithocholic acid (solid triangles) on CO_2 responses. Control responses to CO_2 before adaptation are shown by solid circles.

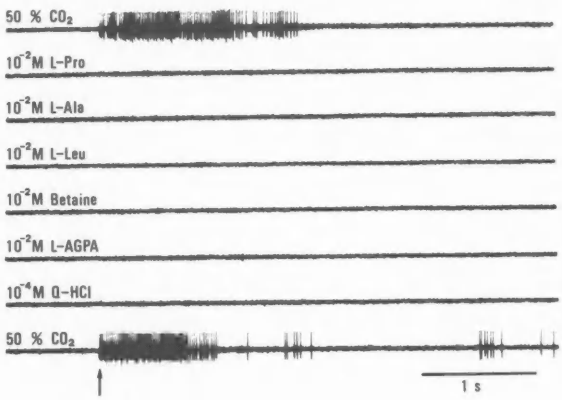

FIG. 6. Single unit recordings of a CO_2-sensitive palatine nerve fiber. The arrow indicates the onset of stimulation.

To examine whether receptors, or fibers, sensitive to CO_2 differ from those which detect other gustatory stimuli, a concentration series of CO_2 was tested while the receptors were adapted to 10^{-3} mol·L^{-1} *L*-proline or 10^{-8} mol·L^{-1} taurolithocholic acid (phosphate-buffered, pH 5.0). These chemicals represent respectively the amino acid and bile salt. Adaptation to either stimulant had little effect on the responsiveness to CO_2 (Fig. 5).

Single palatine nerve fibers spontaneously firing were isolated. They were easily distinguishable from those fibers sensitive to amino acids owing to their high firing amplitude and increased frequency upon stimulation with CO_2 solution (Fig. 6). None of the CO_2-sensitive fibers identified responded to *L*-proline, *L*-alanine, *L*-leucine, *L*-α-amino-β-guanidinopropionic acid (*L*-AGPA), and betaine (all at 10^{-2} mol·L^{-1}), but two fibers responded to 10^{-4} mol·L^{-1} quinine–HCl (Table 1).

TABLE 1. Gustatory responses of single fibers of the palatine nerve (VIIth cranial nerve) to CO_2, and other chemical and tactile stimulation in rainbow trout (*Oncorhynchus mykiss*). + = increased firing frequency; − = no response.

Fiber	CO_2	*L*-Proline	*L*-alanine	Betaine	TLCA*	Quinine-HCl	Touch
1	+	−	−	−	−	+	−
2	+	−	−	−	−	−	−
3	+	−	−	−	−	−	−
4	+	−	−	−	−	−	−
5	+	−	−	−	−	+	−
6	−	+	+	−	−	−	−
7	−	−	−	−	+	−	−
8	−	−	−	−	−	−	+
9	−	−	−	+	−	−	
10	−	−	−		+	−	

*Taurolithocholic acid.

Discussion

The present study demonstrates that the rainbow trout gustatory system is highly sensitive to CO_2. Distinct responses by single palatine nerve fibers to H^+ or CO_2 support the claim that fish gustatory receptors are capable of distinguishing CO_2 from H^+ (Hidaka 1970; Yoshii et al. 1980). The threshold concentration of CO_2, 4×10^{-5} mol·L^{-1}, determined for rainbow trout generally agrees with that obtained in the Japanese eel (*Anguilla japonica*) palatine nerve (Yoshii et al. 1980) and with the behavioral CO_2 avoidance threshold for Arctic char, *Salvelinus alpinus* (Jones et al. 1985). This is slightly higher than the level of CO_2 (1.8×10^{-5} mol·L^{-1}) in natural waters which are equilibrated with air.

The concentration–response relationship for CO_2 obtained in the present study clearly shows two discrete components. The response increases slowly over the lower concentration range up to 2×10^{-3} mol·L^{-1}, then sharply rises with further increase in the CO_2 concentration, suggesting the involvement of two separate receptor systems. These results are in contrast with those for the eel, in which the responses increased linearly with logarithmic increase in CO_2 concentration over a range from 2×10^{-5} to 2×10^{-2} mol·L^{-1} (Yoshii et al. 1980). However, Yoshii et al. (1980) argue that because the linear relationship holds over more than two log units, CO_2 either binds to several receptor sites with different binding constants or the binding of CO_2 to one receptor site decreases the affinity of the surrounding site for CO_2 (negative cooperativity). The two-step neural response may be related to a biphasic locomotor response to CO_2 gradient demonstrated in Arctic char (Jones et al. 1985). Carbon dioxide gradients lower than 53 μmol·L^{-1} were attractive for char, but stronger gradients were avoided.

Although responses to lower concentrations (10^{-5} to 10^{-3} mol·L^{-1}) of H^+ were small in magnitude, the duration of the responses (10 to 15 s after rinsing) exceeded 10 times that of the standard response to 10^{-3} mol·L^{-1} *L*-proline (pH 7.8). The concentration–response curve for hydrochloric acid revealed an inflection approximately at pH 3.0. The threshold for H^+ again approximates the electrophysiological result (eel; Yoshii et al. 1980) and behavioral avoidance (Arctic char; Jones et al. 1985).

The result that adaptation to 10^{-3} mol·L^{-1} *L*-proline or 10^{-8} mol·L^{-1} taurolithocholic acid had little effect on the CO_2 response suggests that the receptor(s) for CO_2 are distinct from those for amino acids and bile salts, two known gustatory stimulants in fish (Marui et al. 1983; Hara et al. 1984). This is further supported by the findings from single fiber experiments: (1) firing of fibers sensitive to CO_2 had generally higher amplitude relative to those sensitive to amino acids, and (2) none of the CO_2-sensitive fibers responded to other gustatory stimulants, except two fibers responding to quinine. Such a highly sensitive, specific receptor system for CO_2, independent of other receptors essential for detecting, e.g. food substances, would allow fish to detect and respond to minute changes in CO_2 concentration even under adverse environmental conditions.

Jones et al. (1985) demonstrated that Arctic char have two means of avoiding acidified discharges, a highly sensitive, negative reaction to CO_2 and a supplementary negative response to H^+. Such a dual avoidance system would undoubtedly be more adaptive than one dependent on either factor alone. The avoidance of CO_2 is most likely a behavioral strategy functioning primarily in preventing respiratory distress.

Available evidence suggests that the gustatory system is principally responsible for CO_2 detection in fish. Powers and Clark (1942) had once stated that CO_2 receptors may be located in the lateral-line organs. However, the removal of olfactory tissues and the sectioning of the nerves innervating the lateral-line organs had no effect on behavioral reactions to CO_2 in roach (*Leuciscus rutilus*), minnow (*Phoxinus phoxinus*), and Atlantic salmon (*Salmo salar*) (Höglund 1961). Because striking similarities exist in chemical response profiles between the facial (VIIth) and oro-pharyngeal (IX–Xth) gustatory systems despite their anatomical distinction (Kanwal and Caprio 1983; Kanwal et al. 1987), it is unlikely that the separate gustatory systems, i.e. facial, glossopharyngeal, and vagal, have functional differentiation with regard to CO_2 detection capability. Shelton's (in Hughes and Shelton 1962) demonstration that substantial ventilatory changes in response to CO_2 persisted after total denervation of the gill area by section of the IXth and Xth cranial nerves partly supports this view.

The role of the gustatory chemoreceptors as avoidance mechanisms involved with behavior seems plausible. Despite a large volume of information on the central pathways of the gustatory system in fishes (Marui 1986), basic concepts of the neural structure and function require experimental protocols utilizing more essential chemical stimuli. The importance of gustation in detecting environmental chemicals other than feeding stimuli may be much greater than generally believed (Segaar et al. 1983; Yamamori et al. 1987; Yamamori et al. 1988).

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Effects of Fertilization and Planktivorous Fish on Epilimnetic Phosphorus and Phosphorus Sedimentation in Large Enclosures

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Enclosure experiments were conducted during 1986 and 1987 to test the hypothesis that predation-induced shifts in plankton size-structure affect epilimnetic total phosphorus (TP) through changes in sedimentation rates, both with and without external nutrient loading. Fertilization and/or planktivorous fish were applied to eight enclosures in a 2 × 2 factorial design. Epilimnetic TP was higher with fish in the unfertilized enclosures and lower with fish in the fertilized enclosures; that is, fertilization increased epilimnetic TP only in enclosures without fish, and much less than expected based on the amounts added. The fraction of TP sedimenting per unit time, and the spring to summer decline in TP, was consistently lower with fish. Sedimentation rates were poorly correlated with epilimnetic TP, but were more strongly correlated with TP decline rates and particulate phosphorus larger than 20 μm. Presence or absence of planktivorous fish can alter the trophic status of planktonic systems, and the impact of external nutrient loading by changing the size-distribution and biomass of plankton.

En 1986 et 1987, des expériences ont été réalisées en enclos pour vérifier l'hypothèse que les modifications de la structure par taille du plancton dues à la prédation influent sur le phosphore total (PT) de l'épilimnion en provoquant des changements dans les taux de sédimentation, qu'il y ait ou non apport externe de substances nutritives. Dans le cadre d'un plan d'expériences factoriel 2×2, on a mis des fertilisants et ou des poissons planctivores dans huit enclos. Le PT de l'épilimnion était plus élevé quand il y avait du poisson dans les enclos non fertilisés et plus faible quand il y avait eu du poisson dans les enclos fertilisés; autrement dit, la fertilisation a fait accroître le PT de l'épilimnion seulement dans les enclos ne contenant pas de poisson et beaucoup moins que prévu d'après les quantités ajoutées. La partie de PT qui se dépose par unité de temps et la baisse de PT observée du printemps à l'été étaient de façon constante plus faibles lorsqu'il y avait du poisson. Les taux de sédimentation corrélés avec le PT de l'épilimnion, mais il l'étaient plus fortement avec les taux de diminution du PT et le phosphore particulaire d'un diamètre supérieur à 20 μm. La présence ou l'absence de poissons planctonivores peut modifier le statut trophique des communautés planctoniques et les répercussions de l'apport externe de substances nutritives en changeant la répartition par taille et la biomasse du plancton.

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Reducing phosphorus input has been used successfully to reverse lake eutrophication (Vollenweider 1968: Edmondson 1969; Schindler 1975, 1977; Hurley et al. 1986). However, the emphasis on external phosphorus loading as a determinant of the phosphorus content of lakewaters and eutrophication has obscured the importance of food web interactions. Wright and Shapiro (1984) reported that epilimnetic total phosphorus (TP) declined following a shift from small-bodied to large-bodied herbivorous zooplankton, and concluded that vertical migration of zooplankton may be responsible for the transport of phosphorus to the hypolimnion. However, they did not measure the sedimentation of material in their manipulation experiments.

Earlier studies have suggested that sedimentation of particles from the epilimnion is a major process regulating epilimnetic TP (White and Wetzel 1975; Charlton 1975; Fallon and Brock 1980), but the mechanisms controlling sedimentation rates have rarely been studied. Sinking of algae has been reported as an important factor controlling their abundance in the epilimnion, especially in the spring when diatoms predominate (Ulen 1978; Sommer 1984; Scavia and Fahnenstiel 1987). Grazing by herbivorous zooplankton is also known to effect the sedimentation of algae (via faecal pellet production) from the epilimnion (Bürgi et al. 1979; Scavia and Fahnenstiel 1987; Uehlinger and Bloesch 1987).

Although some work has been done on sedimentation in lakes as affected by increased external loading (Charlton 1975) and by changes in community structure (Bürgi et al. 1979; Uehlinger and Bloesch 1987), the importance of sedimentation in controlling epilimnetic TP, and the mechanisms controlling sedimentation, are poorly understood. Here we examine temporal changes in epilimnetic TP, and their relationship to phosphorus sedimentation, in large enclosures. We test the hypothesis that predation-induced shifts in plankton size-structure affect sedimentation rates and, therefore, epilimnetic TP, both with and without external nutrient loading.

Materials and Methods

Experimental Design

This study was conducted during the summers of 1986 and 1987 at Lake St. George, Ontario. Eight large experimental

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enclosures (8 m diameter, 15 m deep, and open at the sediment) were used to evaluate two treatments, nutrient and/or planktivorous fish addition, in a 2×2 factorial design (see Mazumder et al. 1988 for details). Details of the enclosures are described in Post and McQueen (1987). Prior to the experiments, fish were removed from all enclosures with a purse-seine and, to create similar preexperimental conditions, the enclosures were flushed with 600 m^3 of water from the lake. Depths of the thermoclines in the enclosures, defined as depth of maximum temperature change, were between 4 and 7 m in late spring and summer.

The enclosures were divided into two groups, nonfertilized and fertilized. Nutrients (N and P, 13:1) were dissolved in water and were added to the epilimnion (0–4 m) using a garden hose. The hose was kept in constant motion, both vertically and horizontally, to ensure even distribution of nutrients in the entire epilimnion. The fertilized enclosures received weekly additions of 3.69 mg $P \cdot m^{-2} \cdot d^{-1}$ (added as H_3PO_4) and 48.3 mg $N \cdot m^{-2} \cdot d^{-1}$ (added as $NaNO_3$) from April 28 to August 12 in 1986, and May 6 to August 10 in 1987. Each weekly addition was enough to increase epilimnetic TP and total nitrogen (TN) by 6.46 μg $P \cdot L^{-1}$ and 84.54 μg $N \cdot L^{-1}$.

Two enclosures from each group (unfertilized and fertlized) were stocked with 62.8–68.6 $kg \cdot ha^{-1}$ of 1+ yellow perch (86–94 fish per enclosure with a mean wet weight of 3.65 g) on May 31 (1986) and with 35–38 $kg \cdot ha^{-1}$ (50–55 fish per enclosure with mean wet weight of 2.92 g) on April 27 (1987). All added fish were marked, and were recaptured three times during each summer. Fish killed by handling were replaced with similar-sized fish from the lake. No fish were lost, and only three small unmarked fish were found and removed.

Unfertilized enclosures with and without fish were designated as "+F" and "control", while fertilized enclosures with and without fish were designated as "+NF", and "+N". Details of experimental design are described in Mazumder et al. (1988).

Determination of Epilimnetic Phosphorus (TP)

Dissolved phosphorus and particulate phosphorus in different size-fractions were measured in replicate 0–4 m tube samples (6.5 cm diameter) on six sampling dates in 1986 and four dates in 1987 (May through August). Dissolved and particulate phosphorus in 10 size-classes (<0.2 μm to >400 μm) were analyzed following filter fractionation (see Mazumder et al. 1988 for details). Concentration of phosphorus in each size-class was determined after oxidation under pressure (Menzel and Corwin 1965) with the ascorbic acid modification of the molybdenum blue method (Strickland and Parsons 1972. Epilimnetic TP concentration was determined by adding the concentrations of phosphorus in all size-classes. TP was also determined for triplicate whole water samples collected with Van Dorn bottles from 8 m. Accumulation of phosphorus by fish was measured by analyzing phosphorus contents of 15 fish on three dates in 1986 and 1987 (initial, 17 July, and 25 August). Loss of phosphorus into periphyton growth was measured by analyzing the phosphorus content of vertically-oriented substrata (made of the same material as the enclosure wall) on three dates in 1987 (25 June, 15 July, and 12 August). See Mazumder et al. (1989) for details on periphyton phosphorus.

Phosphorus Sedimentation

Sedimentation of material from the epilimnion is usually measured using sediment traps. These may accurately measure sedimentation in certain lakes, especially in deep stratified lakes. Charlton (1975) demonstrated that sedimentation rates of phosphorus measured in large enclosures are consistent with those measured in open lake water. Enclosures used in this study are deep and show strong thermal stratification during late spring and summer periods. Therefore, cylinder-type sediment traps (Bloesch and Burns 1980) should provide a reliable estimate of the actual loss of material from the epilimnion to the hypolimnion.

Four (two pairs) cylindrical sediment traps (6.5 cm diameter, 40 cm long, aspect ratio of 1:6) were set below the thermocline (8 m) in each enclosure in 1986 (June 3–August 19). Six traps (one central pair floating at 8 m from an anchor, one central pair hanging from the top and one pair hanging 1 m away from the enclosure wall) per enclosure were used in 1987 (June 25–August 10). Each pair of traps was attached to the ends of a 1-m steel bar suspended with a nylon rope tied to a float at the surface. The pairs of traps suspended from an anchor, rather than from the surface, and the pair of traps hanging from the wall, were used to ensure that sedimentation rates were not higher below the ropes or near the walls.

Sediment trap samples were collected every 2–3 wk in both years. At the time of collection, the traps were pulled up very slowly, and the water in the traps was decanted to leave 1 L, stirred thoroughly, and two 35-mL subsamples were collected in clean screw-capped test tubes. Samples (100 mL) were also collected (1987 only) and preserved with Lugol's iodine solution for microscopic observation. Samples collected during the July–August period of 1987 were used for microphotography; 5-mL subsamples were settled in Utermöhl chambers and photographed at 200× using an inverted phase microscope. Concentrations of phosphorus in the subsamples (two per trap) was measured following the method described above. Measured TP concentrations in the sediment trap samples were corrected for the ambient TP at 8 m.

Determination of Total Epilimnetic Calcium

Concentrations of total calcium (milligrams per litre) were determined from 0–4 integrated water samples. Collected samples were analyzed at Water Quality National Laboratory, Environment Canada, Burlington, Ontario.

Statistical Analysis

Analyses of variance (ANOVA) were performed for TP (milligrams phosphorus per square metre) and sedimentation rates (milligrams phosphorus per square metre per day and percent TP per day) for all sampling dates. Repeated measures ANOVA (Model III ANOVA) were also performed for all dates taken together for each year. Prior to calculating confidence intervals or standard errors, variance ratio tests (Zar 1984) were done to examine whether the variances were different between replicate enclosures or overall. Simple regressions were performed to test the relationships between sedimentation rates and TP, and particulate phosphorus (PP) >20 μm, and multiple regressions were performed to predict sedimentation rates from the size-distribution of PP and hypolimnetic TP.

Results

Epilimnetic TP

In 1986, the seasonal mean TPs were 74.4, 88.6, 114.2, and 88.5 mg $P \cdot m^{-2}$ in the control, +F, +N, and +NF

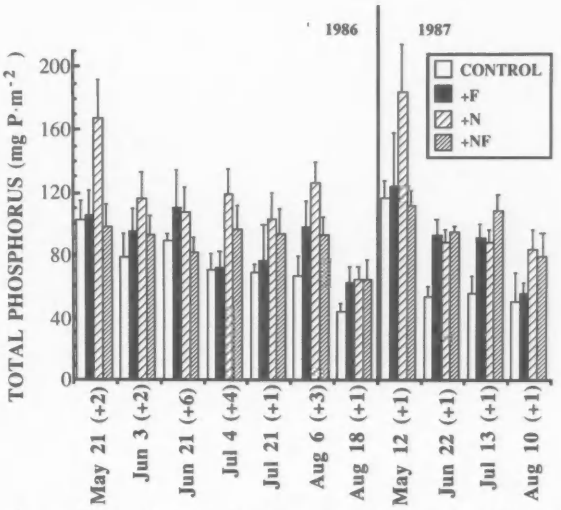

FIG. 1. Epilimnetic TP in four treatments. Bars represent 95% CI of the pooled mean of four (two per replicate enclosure, degree of freedom = 2) measurements. TP (mg $P \cdot m^{-2}$) = TP (μg $P \cdot L^{-1}$) × 4 m. Numbers associated with sampling dates represent the number of days lapsed between fertilization of enclosures and sampling for TP.

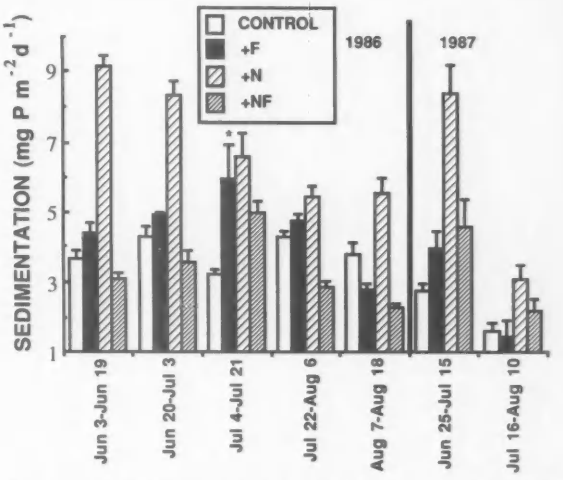

FIG. 2. Sedimentation rate of phosphorus in four treatments from June to August, 1986 and 1987. Error bars represent 95% CI of the pooled means ($df = 6$ for 1986, and 10 for 1987). * = 95% CI was calculated from the means of replicate enclosures with one degree of freedom, because the variances were different between replicate enclosures within treatment.

enclosures, respectively. TP was higher (Fig. 1) with fertilization than without only on July 4, July 21, and August 18 (ANOVA, $p<0.05$). On other dates (May 21, June 3, 21, August 6), although TP was highest in the +N enclosures, significant effects of fertilization were not obtained because the TP in +NF enclosures was lower than in the control and/or +F enclosures. The effect of fish on TP was reversed by fertilization. As a result, the effect of fertilization and fish on TP over the whole season had significant interaction (repeated measures ANOVA, $p<0.04$; Fig. 1).

There was a decline in TP [TP decline = $\{(TP_1 - TP_2 + (TP_2 - TP_3) + \ldots\} \div t$; where TP_1 to TP_n = epilimnetic TP on first to nth sampling dates, and t = total number of days from first to nth sampling date, during the spring to summer experimental period in all treatments. Although the timing of this decline varied among treatments, and between years for the control enclosures, the TP declines during the experiments were higher in the fishless enclosures; 0.65, 0.48, 1.15, and 0.37 mg $P \cdot m^{-2} \cdot d^{-1}$ for control, +F, +N, and +NF enclosures, respectively.

In 1987, epilimnetic TP trends among treatments were remarkably similar to those in 1986. However, seasonal mean TP was significantly higher with fertilization (repeated measures ANOVA; $p = 0.004$). Seasonal TPs were 69.4, 91.4, 111.4, and 98.2 mg $P \cdot m^{-2}$ in the control, +F, +N, and +NF enclosures, respectively. On one date (August 10) TP was higher with fertilization ($p = 0.001$) in enclosures both with and without fish. On the other dates, +F enclosures had TP greater than at least one of the two fertilization treatments. As a result, fertilization and fish again had significant interaction on three dates ($0.019 < P < 0.03$, Fig. 1). The rates of TP decline in the different treatments were similar to those in 1986, but slightly higher in the unfertilized enclosures; 0.77, 0.74, 1.13, and 0.36 mg $P \cdot m^{-2} \cdot d^{-1}$ for control, +F, +N, and +NF enclosures, respectively. The fishless enclosures (control and +N) again had higher TP declines.

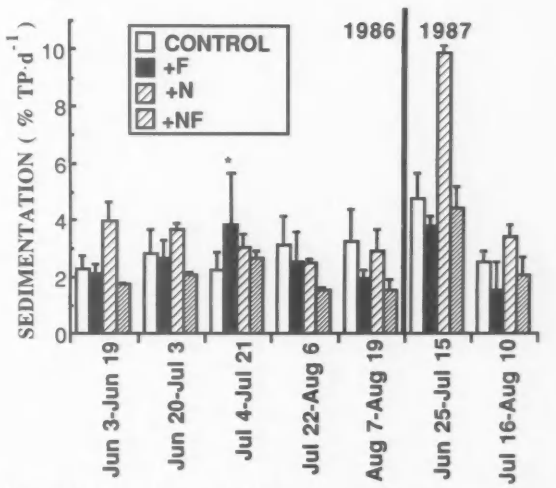

FIG. 3. Sedimentation rate in four treatments from June to August, 1986 and 1987, expressed as a percent of the TP at the beginning of the measurement period. Error bars represent 95% CI of the pooled means. * is same as in Fig. 2.

Sedimentation of Phosphorus

The rates of TP decline (PD) were strongly related with phosphorus sedimentation rates (SR) (SR = 1.66 + 3.67 PD, $r^2 = 0.67$, $n = 16$). However, when unfertilized and fertilized enclosures were analyzed separately, the relationship for fertilized enclosures was SR = 2.36 + 3.31 PD ($r^2 = 0.87$), while a much weaker relationship (SR = 0.44 + 4.83 PD, $r^2 = 0.47$) with a smaller y-intercept and a larger regression coefficient was found for unfertilized enclosures.

Sedimentation rate (milligrams phosphorus per square metre per day), as measured by the traps, was usually higher with fish

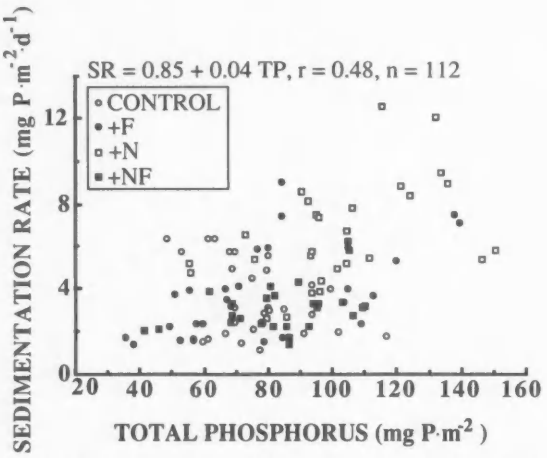

FIG. 4. Relationship between sedimentation rate (SR) and epilimnetic TP. Data include seven collection periods (1986 and 1987) for four treatments.

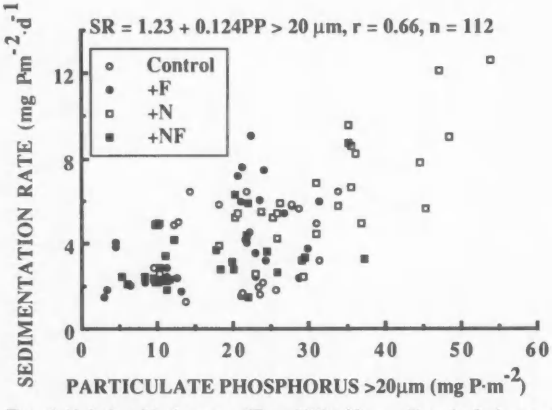

FIG. 5. Relationship between SR and PP>20 μm. Data include seven dates (1986 and 1987) for four treatments.

in the unfertilized (+F) enclosures, and lower with fish in the fertilized (+NF) enclosures (Fig. 2). As a result, significant interactions for the effects of fertilization and fish were obtained on most dates (ANOVA, $0.001<p<0.034$). On average, sedimentation rates were 4.56, 3.86, 7.03, and 3.35 in 1986 and 2.17, 2.70, 5.72, and 3.39 mg $P \cdot m^{-2} \cdot d^{-1}$ in 1987 for control, +F, +N, and +NF enclosures, respectively.

The interaction of fish and fertilization was removed by expressing sedimentation as a fraction of the epilimnetic TP (percent TP per day) (Fig. 3). The effect of fertilization on fractional sedimentation rates (1986 and 1987) was not significant (repeated measures ANOVA, $p=0.161$), but the effect of fish was significant ($P=0.026$). The fraction of TP sedimented was significantly lower ($0.001<P<0.05$) in the enclosures with fish (+F and +NF) on all dates except July 21, 1986 in the +F enclosures. On this date, the two replicate +F enclosures had significantly different means and variances, and for that reason confidence intervals were calculated using the means of the two replicate enclosures with one degree of freedom (Figs. 2 and 3). This may have produced significant interaction for the effects of fertilization and addition of fish on that date ($p=0.007$).

Sedimentation rates were positively related with epilimnetic TP (Fig. 4). However, this relationship explained only 23% ($p<0.01$) of the variation in sedimentation rate. Sedimentation rate was more strongly related with the >20 μm fraction of PP (Fig. 5). There was no significant relationship between sedimentation rate and PP <20 μm. Multiple regression was used in an attempt to relate SR to the amount of phosphorus in various size-fractions. A regression coefficient of near zero was found for PP 0.2–20 μm, and the coefficient for PP 20–200 μm was higher than that for PP>200 μm. The model

$$(1)\quad SR = 1.167 + 0.001(PP\ 0.2-20) + 0.175(PP\ 20-200) + 0.121(PP>200),$$

did not improve the prediction of sedimentation rate (multiple $r^2=0.45$, $n=112$). The residuals between the measured and predicted SR were only 5 to 7% for the unfertilized enclosures, but were 10 to 25% for fertilized enclosures. Examination of the residuals indicates that the relationship differs within treatments. The strength of the correlation is primarily among, rather than within, treatments.

The high regression coefficient for the relationship between SR and TP decline, indicating that SR is more than adequate to account for the decline in epilimnetic TP, and the low coefficient of determination of the relationship between SR and TP fractions, suggests there is a source or component of sedimentation not included in this analysis. To investigate whether TP between the epilimnion, as defined by sampling regimen, and the sediment trap at 8 m was the missing source, we repeated the multiple regression equation (1) between SR and TP fractions adding TP at 8 m as an additional independent variable. The multiple regression equation

$$(2)\quad SR = -0.685 + 0.007\ (PP0.2-20) + 0.482(PP20-200) + 0.176\ (PP>200) + 0.024\ (TP\ 8m),$$

had a significantly higher r^2 (0.75). This multiple regression model was used to correct sedimentation rate for the contribution of metalimnetic TP by setting TP at 8 m to 0 and predicting SR.

To verify our rate estimates, we attempted a mass balance of phosphorus in our enclosures for 1987, when we estimated the amount of phosphorus lost as periphyton growth and fish growth. Wet deposition of phosphorus in the vicinity of Lake St. George is also known (0.05 mg $P \cdot m^{-2} \cdot d^{-1}$; Tang et al. 1986). The net imbalance in the phosphorus budget is expressed as internal loading (Table 1). Calculated internal loading was higher in the fertilized enclosures, enclosures with fish had higher internal loading than in the enclosures without fish.

Sedimenting Materials

Photographs of sediment trap material from different treatments illustrate the qualitative effects of the treatments on the particles sedimenting from the epilimnion (Fig. 6). Sedimenting particles in fishless enclosures were larger than those in the enclosures with fish. Aggregated materials, possibly faeces, were common. Identifiable algae from the control trap were mostly *Ankistrodesmus falcatus*, the diatom *Achnanthes*, and *Dinobryon* loricae. In the +N trap, dominant genera were *Gleocystis* and *Oocystis*. Many of the cells had prominent sheaths, and appeared to be resistant stages. In the +F enclo-

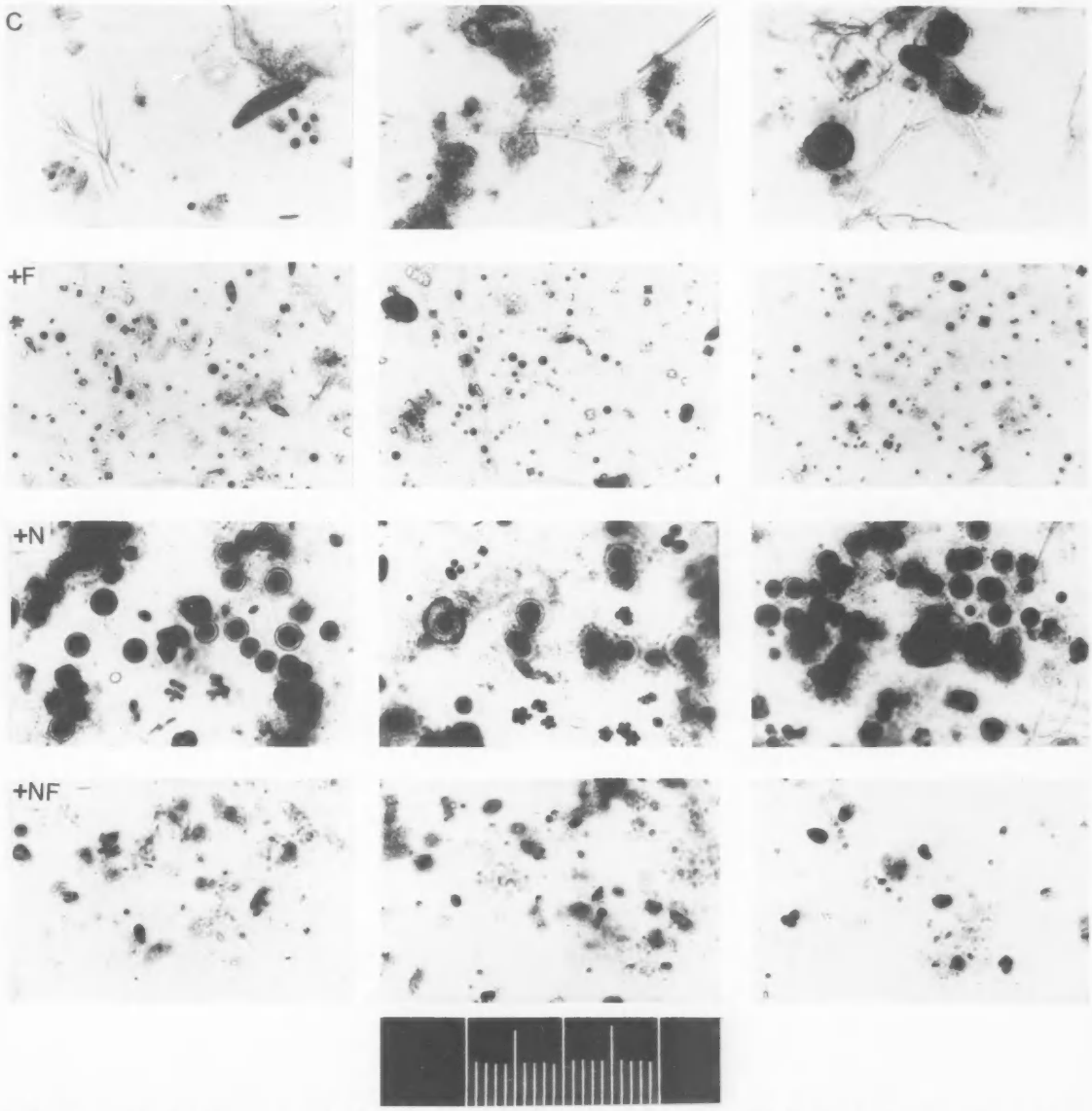

FIG. 6. Photographs of sediment trap material from July–August 1987 preserved with Lugol's iodine. Each row is from one treatment; from top to bottom, control, +F, +N, and +NF. Smallest unit in the scale is equal to 10 μm.

sures, most of the material in the sediment trap examined was nanoplankton. These were predominantly *Scenedesmus* and other green algae in +F enclosure, while *Lagerheimia* and *Chroococcus* dominated the +NF sample. In the +NF enclosures, sedimenting algal cells were generally larger than those in the +F enclosures. Most of the cells from both +F and +NF traps appeared to have intact chloroplasts. Aggregations of cells, possibly faecal material, were more common in the +NF treatment.

Epilimnetic Calcium

There were treatment differences in the amount of epilimnetic calcium in both years (Fig. 7). Calcium was less in the presence of fish and with fertilization. White sediment that we believe to be calcite was observed in +F, +N, and +NF traps in summer.

Discussion

Fish reduced the fraction of epilimnetic TP sedimenting per day, and the seasonal decline in TP, both with and without fertilization. However, there was strong interaction between our two treatments; fertilization was more effective in increasing epilimnetic TP in the absence of fish, but addition of fish was associated with an increase in TP in unfertilized enclosures. Fertilization and addition of fish also had interactive effects on

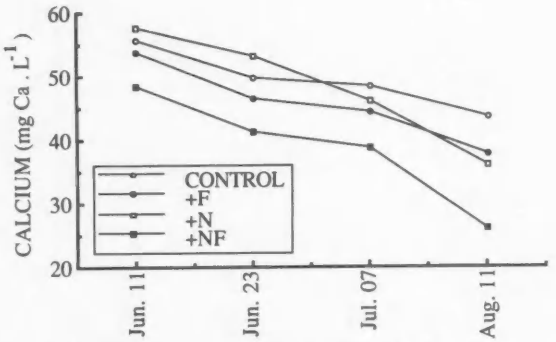

FIG. 7. Temporal changes in the total epilimnetic (0–4 m) calcium concentrations in four treatments on four dates in 1986. Each point is a mean of two determinations (one per enclosure).

sedimentation rate. However, these interactions were removed when sedimentation rates were expressed as fraction of TP sedimenting per unit time.

Our results from unfertilized enclosures support Wright and Shapiro's (1984) observation that TP can be reduced through a shift from small to large grazers, although the opposite result was obtained in fertilized enclosures. In enclosures without planktivorous fish, body lengths of cladocerans, especially *Daphnia*, were greater (A. Mazumder, unpubl. data), and about 54–57% of the total PP was present as microplanktonic and mesoplanktonic particles (20–200 μm and >200 μm, Mazumder et al. 1988). In contrast, in the fish enclosures (+F and +NF), only 36–37% of the total epilimnetic particulate phosphorus was comprised of these larger particles, and most of the particulate phosphorus was pico- and nanoplankton (0.2 to 20 μm). We observed higher seasonal epilimnetic TP declines in the fishless enclosures with larger zooplankton.

Our results suggest that fractional sedimentation of TP can be affected by food web changes. Fractional phosphorus sedimentation was reduced by planktivorous fish, but our measured rates are within the range reported from lakes (White and Wetzel 1975; Fallon and Brock 1980; Bloesch and Uehlinger 1986; Scavia and Fahnenstiel 1987) and enclosures (Charlton 1975; Uehlinger and Bloesch 1987). For example, our corrected mean sedimentation rates were 1.01 and 3.23% $TP \cdot d^{-1}$ in the Control and +N enclosures, while Charlton (1975) reported 2.1% $TP \cdot d^{-1}$ (5.9 mg $P \cdot m^{-2} \cdot d^{-1}$) and 2.8% $TP \cdot d^{-1}$ (13.6 mg $P \cdot m^{-2} \cdot d^{-1}$) in control and fertilized enclosures, respectively. Higher phosphorus sedimentation rates (4–5%$\cdot d^{-1}$) were estimated from a budget model by Stauffer (1985) for two calcareous lakes in Wisconsin. In Toussaint Lake and Lindsey Pond, the daily losses of phosphorus were 1 and 2%$\cdot d^{-1}$ (Rigler 1973). He suggested these rates may be similar among lakes. Vollenweider (1969a,b) assumed a loss of phosphorus proportional to epilimnetic TP in his phosphorus budget model for lakes. Although Wright and Shapiro (1984) speculated that enhanced vertical transport by herbivores was responsible for TP decline, Nilssen (1978) and Taylor (1984) suggested that large herbivorous zooplankton enhance sedimentation, while Bürgi et al. (1979) and Uehlinger and Bloesch (1987) demonstrated that higher sedimentation rates were associated with abundant large herbivores. In Lake Michigan, changes in the abundance of large grazers (*Daphnia*), associated with changes in planktivore predation, may have caused changes in epilimnetic TP and sedimentation rate (Scavia et al. 1986; Scavia and Fahnenstiel 1987).

TABLE 1. Sources and losses for phosphorus (seasonal means) for four treatments in 1987. All values except TP at 8 m are in mg $P \cdot m^{-2} \cdot d^{-1}$. TP loading = wet depositon + weekly additions. Expected net loss from the epilimnion = loading − (loss of periphyton + fish) + TP decline. Internal loading = corrected sedimentation rate − expected net loss from the epilimnion.

	Control	+F	+N	+NF
TP loading	0.05	0.05	3.74	3.74
Loss to fish	—	0.57	—	0.54
Loss to periphyton	0.50	0.60	0.60	0.90
Observed TP decline	0.77	0.74	1.13	0.36
Expected net loss from the epilimnion	+0.32	−0.38	+4.27	+2.66
Measured SR	2.17	2.70	5.72	3.39
TP at 8 m (μg $P \cdot L^{-1}$)	59.9	112.9	70.2	43.3
Corrected SR for TP at 8 m	1.01	0.70	3.23	1.41
Internal loading or net imbalance	+0.69	+1.08	+1.04	+1.25

Our sedimentation rates overestimated phosphorus loss from the epilimnion because biological incorporation of dissolved phosphorus into particulate phosphorus in the 4–8 m zone contributed to sedimentation at 8 m. Both sedimentation rates and metalimnetic TP were highest in the unfertilized enclosures with fish (+F) and in fertilized enclosures without fish (+N). In the +N enclosures, high TP at 8 m may have been due to development of phytoplankton as the water was oxic and light intensity was high. In the +F enclosures, where this depth was anoxic and light intensity was low, there was a dense population of photosynthetic bacteria (A. Mazumder, unpubl. data). Concentration of TP at this depth was higher than the epilimnetic TP among all treatments, the highest concentration was observed in the +F enclosures (Table 1).

Changes in epilimnetic TP seem largely determined by the rate of phosphorus loss from the epilimnion via sedimentation; 64% of the variation in rate of TP decline is explained by the sedimentation rates in the unfertilized and fertilized enclosures. Although fertilized enclosures received weekly nutrient additions, they showed maximum spring to summer declines of epilimnetic TP, and a strong correlation between TP decline and sedimentation rate. External loading was only moderately effective in increasing epilimnetic TP despite our adding enough PO_4 (332 mg $P \cdot m^{-2}$ in 90 d) to triple the total concentrations. Earlier (Mazumder et al. 1988) we demonstrated opportunistic uptake of the added phosphate by large phytoplankton, which probably have high sinking rates (see equation (1); Uehlinger and Bloesch 1987) and are abundant in trap material (Fig. 6). This could be the mechanism by which the added phosphate is removed from the epilimnion.

The mechanism by which fish affect sedimentation may involve the size-distribution of particles, which was strongly affected by the treatments (Mazumder et al. 1988). This is supported by a strong relationship between PP>20 μm and SR (Fig. 5), and the lack of a relationship with PP<20 μm (slope = 0.001, equation (1)). Similarly, Uehlinger and Bloesch (1987) reported specific sedimentation rate of only 0.007$\cdot d^{-1}$ for PP <12 μm, and mentioned that although suspended seston consisted mainly of small particles, material in sediment traps was dominated by large particles. There are various reports regarding the types of material that contribute more to sedi-

mentation. Some have reported that most of the sedimented material is faecal pellets produced by calanoid copepods (Farrante and Ptak 1978), while others have reported that most of the sedimenting material is of algal origin (Ulen 1978). Sedimentation rates reported here were not correlated with biomass of copepods (cyclopoid, calanoid, or both) or other zooplankton. Scavia and Fahnenstiel (1987) found that in Lake Michigan, direct sinking (nonpredatory loss) of algae, especially diatoms, was the important component of sedimenting material in spring, while algae egested by zooplankton were important in summer. The sedimentation rates estimated during our experiments were higher in the spring when grazing activity of zooplankton was low.

The observation that particle size-distribution only partly explains sedimentation rates probably reflects qualitative as well as quantitative differences in the PP size-fractions. Our fractional sedimentation rates can be translated into settling velocities by multiplying them by 8 m, the depth of the trap. Mean settling velocities in the treatments ranged between 0.15 to 0.18 $m \cdot d^{-1}$, and between 0.22 to 0.26 $m \cdot d^{-1}$, in the fish and fishless enclosures, respectively. These are similar to velocities determined for phytoplankton in Lake St. George by a different method (Burns and Rosa 1980). The nature of the particles, such as the shape, ornamentation, density, motility, etc. are also important. For example, Sommer (1984) found diatoms have very high (3.8 to 16.6 $m \cdot d^{-1}$) sinking rates. Green algae and *Aphanizomenon* have lower settling velocities (0.03 to 2.1 $m \cdot d^{-1}$), and flagellates may have zero velocities (Stabel 1987). Burns and Rosa (1980) found a range of low velocities for Lake St. George phytoplankton, which are only loosely related to size, and lower than for detritus. Qualitative differences in the sinking particles are obvious from Fig. 6, and were also suggested for the important microplankton fraction by the interactive nature of the treatments on this fraction (Mazumder et al. 1988).

The net imbalance in the phosphorus budget is expressed as internal loading. Few studies have attributed the discrepancy between epilimnetic TP changes and sedimentation explicitly to internal loading, but internal loading can be large for lakes with anoxic hypolimnia (Stauffer 1985; Lehman and Naumowski 1986). Our mass balance for phosphorus indicates that phosphorus sedimentation, even corrected for metalimnetic TP, is more than adequate to explain TP decline in the unfertilized enclosures. If we overestimated periphyton growth by using substrata that were initially free of periphyton, then our calculated internal loading may be even smaller. The fertilized enclosures had slightly too little sedimentation to account for TP decline, after correcting sedimentation rates for metalimnetic contribution. However, the discrepancy is very small.

The relative importance of calcium minerals as a vehicle for phosphorus transport in our enclosures is unknown. However, we observed that the highest pH and lowest concentration in epilimnetic calcium was associated with presence of fish (Fig. 7), which may be due to the increased abundances of pico- and nanoplankton (Mazumder et al. 1988). Murphy et al. (1983) reported that when calcite precipitation occurred during an *Aphanizomenon* bloom, PO_4 was completely removed from the euphotic zone. Stabel (1987) reported that high sedimentation in Lake Constance was associated with calcite precipitation. Phosphate concentrations in the enclosures were always below detection limit (<0.5 μg PO_4–$P \cdot L^{-1}$), and as a result it is not possible to estimate the amount of phosphorus that may be precipitating with calcium. However, if this was a vehicle for vertical transport of phosphorus, then its effect would be to reduce the treatment effect (reduced percent sedimentation with fish) we observed.

We conclude that food web effects resulting from the presence of planktivorous fish can affect the trophic status of planktonic systems, and that the efficacy of fertilization is dependent on the food web. Planktivorous fish can reduce the loss of phosphorus from the epilimnion by favoring the dominance of smaller plankton which contribute more to total biomass and less to sedimentation.

Acknowledgements

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Capelin (*Mallotus villosus*) Spawning on the Southeast Shoal: Influence of Physical Factors Past and Present

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Carscadden, J. E., K. T. Frank, and D. S. Miller. 1989. Capelin (*Mallotus villosus*) spawning on the southeast shoal: influence of physical factors past and present. Can. J. Fish. Aquat. Sci. 46: 1743–1754.

Co-occurrence of beach- and offshore bottom-spawning populations of capelin (*Mallotus villosus*) in the Northwest Atlantic appears to be unusual. To explain the evolution of bottom-spawning in the offshore spawning population on the Southeast Shoal, we examined relevant substrate, water temperature, and biological data. Published data indicate that the Southeast Shoal was not glaciated during the Wisconsin glaciation (about 20 000 yr ago) and was above sea level. As the glaciers melted, this area was a surf zone before it became inundated. This suggests that this stock was once a beach-spawning stock and supports our hypothesis that substrate is the ultimate factor affecting spawning location. Analysis of 7 yr of distribution, maturity, and bottom temperature data showed that the variation in the final spawning location was not large and spawning occurred where bottom temperatures exceeded approximately 2°C. We conclude that bottom temperature is a proximate factor influencing the final spawning location. Physical data for other areas of the Grand Banks indicate that only the Southeast Shoal has favourable substrate, bottom temperatures and environmental factors subsequent to spawning to allow the long-term survival of a capelin population.

La co-occurrence de populations de capelans (*Mallotus villosus*) frayant sur le fond dans les eaux littorales et hauturières du nord-ouest de l'Atlantique semble inhabituelle. En vue d'expliquer l'évolution de la population frayant sur le fond dans la zone hauturière du Platier, nous avons étudié un ensemble de données pertinentes sur le substrat, la température de l'eau et les facteurs biologiques. D'après les données publiées dont nous disposons, la glaciation du Wisconsin (20 000 an avant l'époque actuelle) n'a pas touché le Platier : celui-ci se trouvait alors au-dessus du niveau de la mer. Lorsque les glaciers ont fondu, cette région était une zone de brisance, puis elle a été inondée. Ces faits indiqueraient que le stock hauturier a autrefois frayé dans la zone littorale ; ils étayent en outre l'hypothèse que nous avons avancée, soit que le substrat est le facteur déterminant du choix du lieu de fraye. L'analyse de données recueillies en 7 an sur la distribution, la maturité et la température du fond a révélé que la variation de l'emplacement final de fraye n'est pas importante et que la fraye se déroule là où la température au fond de l'eau dépasse environ 2°C. Nous en concluons que la température du fond est un facteur à influence immédiate sur le choix de l'emplacemenet du lieu de fraye. D'après des données recueillies sur les caractères physiques d'autres secteurs du Grand Banc, ce n'est que dans le Platier que le substrat et la température du fond seraint favorables et que les facteurs du milieu après la fraye seraient tels que la survie à long terme de la population de capelans serait assurée.

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Capelin (*Mallotus villosus*) are small, pelagic, schooling fish native to the northern hemisphere. They are demersal spawners and their eggs adhere to the spawning substrate. In the Northwest Atlantic, five stocks (or stock complexes) have been identified (Fig. 1) on the basis of spawning times, patterns of fishery, meristics and morphometrics (Campbell and Winters 1973; Carscadden and Misra 1980; Misra and Carscadden 1984, 1987). The Southeast Shoal stock (NAFO (Northwest Atlantic Fisheries Organization) Div. 3NO) mixes and overwinters with the northern Grand Bank/Avalon stock (NAFO Div. 3L) on the northern Grand Banks before migrating to the spawning area (Carscadden 1984), a shallow (about 50 m deep) bank on the southern Grand Banks of Newfoundland, approximately 350 km from the nearest spawning beach. Thus, capelin that spawn on the Southeast Shoal undergo spawning migrations on the order of 300 km between April and June.

With the exception of the Southeast Shoal stock, all of the Northwest Atlantic stocks are beach (intertidal) spawners. For the beach spawners, spawning is sometimes subtidal but this occurs when water temperatures near the beaches become too warm later in the spawning season (Templeman 1948). The existence of both beach-spawning and offshore bottom-spawning populations in open-water areas (i.e. not restricted to fjords or embayments) appears to be unusual; only in the Northwest Atlantic do both modes of reproduction occur. In Alaska and British Columbia, capelin are beach spawners (Pahlke 1985). Capelin in Icelandic waters and the Barents Sea are not beach spawners but spawn on bottom in deeper waters near the coasts (Jangaard 1974). Beach spawning does occur in Norway but in these areas, the capelin spend their entire lives in the same fjord (Nyholmen and Hopkins 1988). Thus, this apparently unusual co-occurrence of capelin with different spawning modes in the

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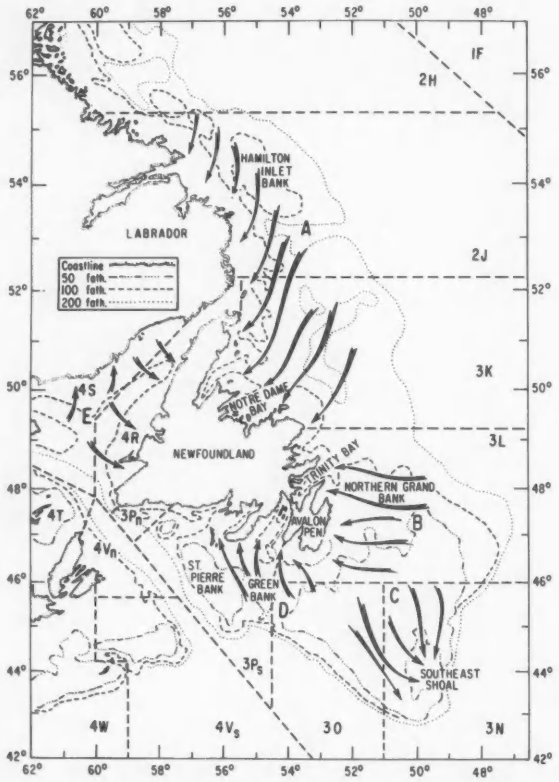

FIG. 1. Map showing major capelin stocks (A–E) and spawning migration routes of capelin in the Northwest Atlantic. Key to stocks: (A) Labrador/Northeast Newfoundland (NAFO Div. 2J3K) stock; (B) Northern Grand Bank/Avalon (NAFO Div. 3L) stock; (C) South Grand Bank (Southeast Shoal; NAFO Div. 3NO) stock; (D) St. Pierre Bank (NAFO Div. 3Ps) stock; (E) Gulf of St. Lawrence stock.

Northwest Atlantic prompted us to investigate the evolution of the two spawning habits and the environmental factors affecting spawning in the two areas. Beach spawning has been reasonably well-described but since there is relatively little information on the factors affecting spawning in the Southeast Shoal population, this paper concentrates on this stock.

Two physical factors, water temperature and gravel sizes, have been previously cited as important for spawning on beaches in Newfoundland and on the bottom on the Southeast Shoal, and capelin have been reported to exhibit different preferences for these physical features in both areas (Sleggs 1933; Templeman 1948; Pitt 1958; Frank and Leggett 1981). The favorable temperature range reported for intensive beach spawning was 5.5 to 7.5°C on the east coast and 6 to 8.5°C on the south coast (Templeman 1948). Sleggs (1933) recorded capelin beach spawning when water temperatures fell between 8.6 and 10.7°C. Frank and Leggett (1981) reported capelin spawning in a wider range of temperatures from 2.5 to 10.8°C. Capelin spawning on the Southeast Shoal was first documented from capelin eggs adhering to sand grains collected from haddock stomachs (Pitt 1958) on two occasions, one each in 1950 and 1951. Bottom water temperatures were reported as 2.8–4.7°C although this was based on only four temperature measurements taken in two years. Carscadden (1978) found that during 1968, 1969, 1975, and 1976, the range of bottom temperatures was 0.1–6.3°C when capelin were spawning.

Templeman (1948) reported that the best spawning beaches had gravel 2–15 mm in diameter, but that spawning occasionally occurred in gravel up to 25 mm in diameter. The sand grains recovered from the stomachs of haddock taken on the Southeast Shoal ranged from 0.5 to 2.2 mm in diameter and in a comparison with beach spawners, Pitt (1958) suggested that capelin have a preferred type of spawning substrate but that the range is wide. Templeman (1965) alluded to the importance of substrate for capelin spawning on the Southeast Shoal. He noted that capelin return annually to the same parts of beaches where the substrate is of a suitable size and appear to return to the same offshore banks which are probably limited in size. He concluded that heavy echo traces near bottom on the Southeast Shoal were capelin spawning on small patches of suitable substrate.

The type and size of substrate in a given area is the result of long-term processes operating over time-scales of centuries and while there may be small, local shifts in sediments (e.g. due to wave action on a beach), the overall geological character of an area can be considered as static when measured in relation to the generation time of capelin (3–4 yr). Thus, geological history determines substrate type and ultimately determines whether a given area will be a suitable spawning site for capelin. Water temperatures, too, will change over centuries (e.g. CLIMAP 1976) and this time-scale will also determine the general suitability of a spawning site. However, temperatures vary on an annual basis and may affect the final location and intensity of spawning in an area where suitable substrate occurs.

We suggest that the ultimate control of spawning on the Southeast Shoal is suitable substrate. In this paper we first examine the possibility that capelin spawning on the Southeast Shoal is the historical consequence of geological evolution because this is intimately tied to substrate morphology. In this analysis, we draw upon relevant literature to make inferences on this possibility and several years of hydroacoustic data to determine the mean geographical position of the spawning stock. Next, we assess the influence of bottom temperature as a proximal factor on the final spawning location by providing a detailed analysis of interannual variability in spawning distribution and capelin maturity stages in relation to bottom water temperatures over the Southeast Shoal.

Materials and Methods

Our biological and oceanographic data were obtained during hydroacoustic surveys conducted annually by the Department of Fisheries and Oceans, St. John's since 1981 to estimate the biomass of the spawning population of capelin on the Southeast Shoal. The results of these surveys have been extensively used in the stock assessment and management process in NAFO (see NAFO Scientific Council Reports 1982–88).

During 1981–85, surveys of the spawning stock on the Southeast Shoal area were part of a larger survey which also provided estimates of abundance of immature capelin on the northern Grand Banks. Beginning in 1986, an independent Southeast Shoal survey of longer duration was undertaken to provide better temporal and spatial resolution of the spawning population. The acoustic surveys were conducted during the end of June and/or beginning of July (Table 1). The hydroacoustic equipment included a SIMRAD EK400 echo sounder with an Ametek/Straza transducer towed behind the research

TABLE 1. Dates of surveys, proportion of biomass estimated to be mature, maximum and minimum values and sample sizes (n) of bottom temperature (°C), depth (m) and capelin density ($g \cdot m^{-2}$), used in the detailed analysis.

Date of survey	% Mature biomass	Temperature		Depth		Density		n
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	
June 20–28, 1981	93	−0.5	4.5	39	90	0.17	111.57	38
July 1–4, 1982	100	1.0	4.6	50	65	20.97	306.25	9
June 27–July 2, 1983	100	2.7	5.8	40	61	0.21	457.95	28
June 24–28, 1984	95	1.8	6.3	44	64	2.04	139.30	8
June 22–26, 1985	77	−0.3	4.5	52	75	1.53	41.25	12
June 26–July 5, 1986	99	−0.7	3.4	41	69	0.04	269.86	34
June 26–July 5, 1987	99	−1.2	4.8	41	71	0.02	91.39	54

vessel in an underwater towed vehicle. The hydroacoustic data were collected from the sounder and stored on 9-track magnetic tape using a custom-built hydroacoustic data acquisition system (Stevens 1986). The analysis employed standard echo integration techniques (Miller and Carscadden 1984; Miller 1985). The survey design, sampling details, and results are available in Miller et al. (1982); Miller and Carscadden (1983); Miller (1984, 1985, 1986); and Miller and Carscadden (1987, 1988). During 1981, 1983, 1986, and 1987 XBT casts were made at regular intervals throughout the survey and after fishing sets, while in 1982, 1984, and 1985, temperature data were collected only in conjunction with fishing sets.

During the acoustic surveys, midwater trawling sets were conducted to collect biological information on target species. Occasionally, midwater trawl sets and XBT casts were made just outside the actual acoustic survey grid and these have been included in the analysis because of their relevance to the study. A number of biological measurements such as length, sex, age, maturity, and stomach fullness were made on capelin but for this paper only maturity stage is considered. A brief description of each of the maturity stages is as follows: (1) Gonads; appear as thin threads. (2) Maturing; gonads are beginning to develop and external sexual characteristics of males are becoming visible. Since this process often begins in the fall, this stage can be quite long. (3) Prespawning; this stage is reached just prior to spawning. Gonads are full and a light squeeze of the fish results in extrusion of sexual products. (4) Spawning; ripe and running sexual products and/or partially full gonads. (5) Postspawning; capelin at this stage are usually taken on or near the spawning grounds. There may be residual eggs or milt and males will retain secondary sexual characteristics.

We used density (grams per square metre) estimates averaged during 1 h of survey time at a constant speed (equivalent to one estimate per 19 km) to construct eye-fitted contours of the capelin distributions on the Southeast Shoal. Bottom temperatures were also contoured by eye to compare with the capelin distribution.

During the estimation of biomass for assessment purposes, all sets are grouped and estimates by age-groups are calculated for the entire survey area. In some instances immature fish are taken in fishing sets. These fish are usually 1 or 2 yr old and occur in very low abundance (less than 5% by numbers in the total abundance estimate) in most years. In this study it was not possible to reliably delineate the boundaries of areas where immatures occasionally occurred in fishing sets because these data were obtained from discrete fishing sets in contrast to the continuous collection of hydroacoustic data. In the years investigated, mature biomass accounted for approximately 95% of the total biomass (Table 1, range of 77 to 100%). Thus, for purposes of this paper, the densities of capelin are considered to be densities of mature fish.

We also conducted a more detailed analysis of the relationship between capelin density and temperature and depth. For this analysis, the average densities of capelin were calculated from data collected from the period between 20 min before the XBT cast and 20 min after for a total time equivalent to about 12 km. Depth was read from the temperature record.

A visual examination of the scatterplots of capelin density and depth, and bottom temperature and depth, on an annual basis, showed no apparent relationship. Using linear regression analysis, density and depth were negatively correlated in 6 of 7 yr but only one of these negative relationships was significant. In the case of bottom temperature and depth, the relationship was negative in 5 of the 7 yr; two of the negative relationships were statistically significant and one of the two positive relationships was significant. Because there were no consistent patterns, we did not investigate the relationships between density and depth and bottom temperature and depth further.

However, we did note an obvious pattern in the plots of capelin density and temperature. To examine this relationship, we estimated its probability density function (pdf) using a nonparametric kernel method (Silverman 1986). The specific algorithm used was the Cauchy method, which Evans and Rice (1988) found performed better than two other nonparametric algorithms tested, and better than estimating parameters of even the correct functional form, for moderately noisy data. In an extension of this analysis, Rice and Evans (1988) used the Cauchy algorithm to investigate the pdf of recruitment as a basis for a discussion of the management of the cod stock in the southern Labrador Sea and northern Grand Banks. In our analysis, the probability of a particular capelin density is proportional to a decreasing function, $1/[1+x/D^2]$ of the difference (x) between the temperature observed at the capelin density and a reference temperature. The parameter D determines how much the observations at temperatures which are progressively more different from the reference value influence the specific pdf. Its value was chosen using the cross validation approach described by Efron and Gong (1983). We used data from 1981, 1983, 1986, and 1987 when sample sizes were adequate (Table 1) and constructed the capelin density pdf at four reference temperatures of −0.5, 1.5, 3.5, and 5.5°C. The pdf's could be estimated for any temperature of interest; these reference temperatures were selected to cover the range of bottom temperatures observed over the period of the study.

Centroids were calculated from the distribution of capelin densities generated from each hydroacoustic survey. The x coordinate ($\bar{X}$) of the centroid was defined by the location (x_i) in

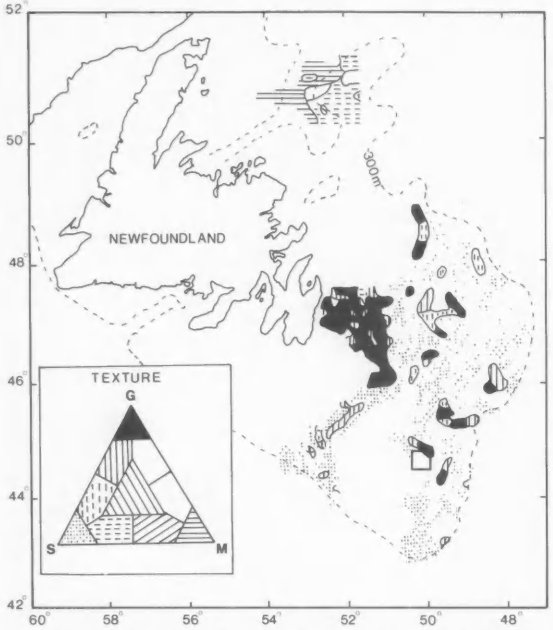

FIG. 2. Distribution of textural types on the Grand Banks (redrawn from Slatt 1974). The square bounds the centroids of capelin densities. G = gravel, M = mud, S = sand.

a defined grid and corresponding capelin density (N_i) using the following relationship:

$$\bar{X} = \Sigma_{i=1,n} N_i x_i / \Sigma_{i=1,n} N_i$$

The Y co-ordinate of the centroid ($\bar{Y}$ was calculated in a similar manner. Therefore, this analysis relates density to geographical location, denoted by latitude and longitude, thereby identifying the centre of mass of the capelin distribution. We used the same densities that were used in the temperature and depth analysis (Table 1).

We also related each of the five maturity stages of capelin to bottom temperatures. Capelin were collected with a midwater trawl and may not have been on bottom when captured. However, capelin are bottom spawners and their presence in the Southeast Shoal area at the time of our surveys is assumed to be ultimately related to spawning and bottom temperature. In addition, temperature stratification, as evidence from long-term data, on the relatively shallow Southeast Shoal is weak during the time of our survey; bottom temperatures are colder than midwater and surface temperatures (Loder and Ross 1988) and the use of bottom temperatures provides information on the minimum temperatures where capelin occur.

Results

Recent Geological History of Grand Banks

During the late Wisconsin glaciation (about 20 000 yr ago) it is believed that the Avalon ice cap extended over the Avalon Peninsula. Slatt (1977) suggests that the rugged topography of the western edge of the Grand Bank acted as a barrier to eastward movement of the glacier. The exact eastward limit of ice has not been clearly defined but Slatt (1977) suggests that it probably occurred at about the present boundary separating gravel and sand (Fig. 2). Large glacial streams probably did not occur and the only significant melting occurred at the north and south edges of the ice where it met the sea. The end result was that the Grand Bank was probably a barren plain with only small glacial streams. During deglaciation, gravel was deposited in the area now adjacent to the Avalon Peninsula. The predominantly sandy area (at present) on the southeastern area of the Grand Banks is of nonglacial origin. It was created by surface erosion and coastal retreat, submergence as the glacier melted and reworking by winter storms and summer/fall tropical cyclones. During the glacial melt, a surf zone would have occurred on the shallowest area of the Bank (i.e. the Southeast Shoal), eroding the coastal cliffs and depositing the sand on the shelf floor. Frosted sand, typical of a beach environment, has been found in the area (Slatt 1973, 1977) supporting the conclusion that there was a passage of a high-energy surf zone across the Southeast Shoal. Thus, during the last 20 000 yr, the Southeast Shoal region (and much of the Grand Banks) was exposed, but as the glaciers melted and receded, the entire Grand Banks became submerged. Being the shallowest area, the Southeast Shoal was the last to become covered with water and during the submergence, the Southeast Shoal or parts of it were an exposed beach.

This description of the evolution of the Grand Banks has been supported by computer models describing global climate during the last 18 000 yr (CLIMAP 1976; COHMAP 1988). The most recent model clearly illustrates that the Grand Banks were above sea level about 18 000 yr ago. By 12 000 yr ago, the Grand Banks were almost completely submerged although the island of Newfoundland was still glaciated.

There are a number of locations on the Grand Banks which have bottom sediments in the range of sizes suitable (Müller and Milliman 1973; Slatt 1974) for capelin spawning (Fig. 2). However, capelin bottom spawning on the Southeast Shoal appears to have evolved because of the unique history of the Grand Banks in the last approximately 20 000 yr. The accumulated information suggests that the Southeast Shoal population was once a beach-spawning population (truly "litophilus" = beach loving (McAllister 1963)), which migrates each summer to an ancestral beach to spawn. In particular, the descriptive model for the late Quaternary depositional history of the Grand Banks (Slatt 1977) provides strong support for this viewpoint.

Mean Geographical Position of Capelin Spawning

Centroids were calculated from point estimates of capelin density and the corresponding latitude and longitude from each of the seven surveys (Table 1). The geographic location of the centres of mass of the distributions were relatively constant over the 7 yr (Fig. 3a) and adjacent to a major deposition of gravel (Fig. 2). The maximum distance between centroids was about 41 km and the centre of distribution of the centroids was located at 44°37′N, 50°12′W. Some caution must be exercised in interpreting the results of this analysis because, in years where more than one area of dense concentration occurred (e.g. 1982, 1986, and 1987), the centroid analysis will produce an "average" area of concentration. Nonetheless, the distributon of capelin in the area was almost constant over the period examined.

Final Spawning Location

Influence of temperature and depth

Bottom temperatures on the Southeast Shoal during late June and early July in 1981, 1986, and 1987 (Fig. 4) showed a pat-

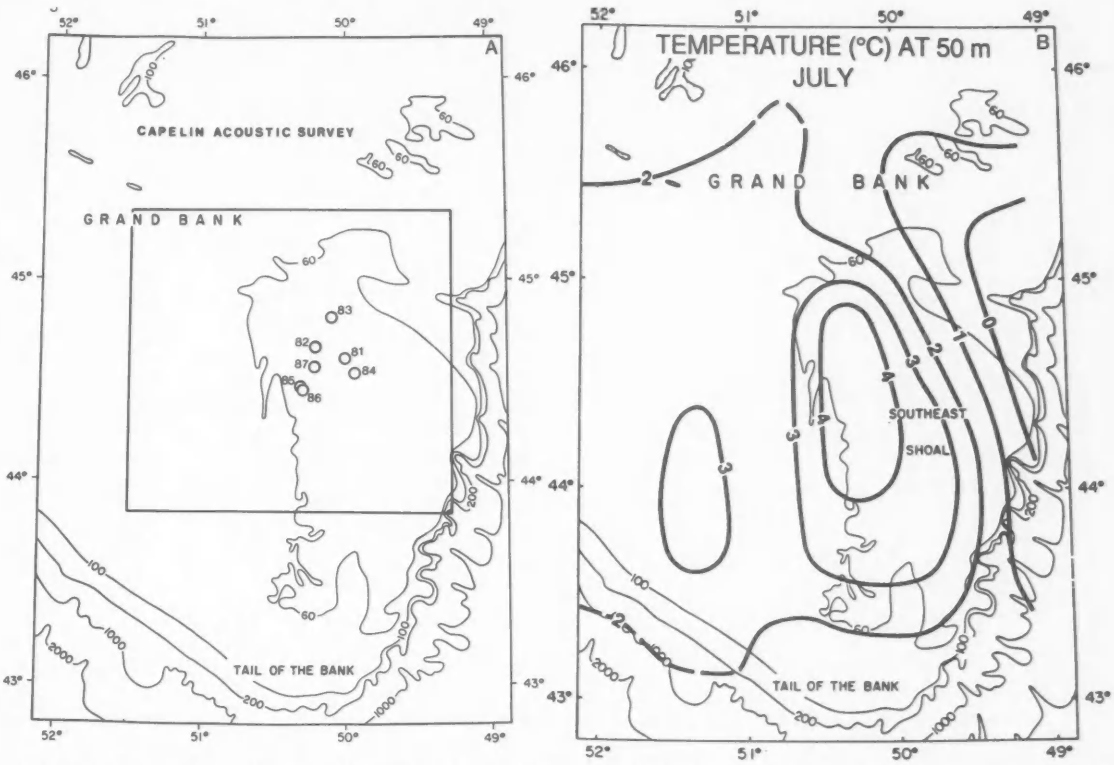

FIG. 3. (A) Centres of densities of adult capelin from 1981–87. (B) Temperature distributions from long-term monthly means at the 50-m level in the Southeast Shoal area during July (from Loder and Ross 1988).

tern similar to the long-term monthly means for July (Fig. 3b). Temperatures on the eastern side of the Shoal were colder, usually less than 2°C, because of the influence of the cold Labrador Current. Temperatures on the central and western part of the Shoal were warmer, usually reaching 4°C and occasionally exceeding 6°C, as was evident in 1984. Although there were few bottom temperature measurements made in 1982 and 1984, temperatures exceeded 4°C in the central part of the Shoal in both years, and in 1984 colder temperatures of 2°C and less were observed in the east and northeast. In 1983, warmer bottom temperatures were observed throughout the study area. In contrast, during the 1985 survey, bottom temperatures less than 2°C extended over a wider area of the Shoal and water above 4°C occurred in only the southern part of the survey area at approximately 44°N.

The distribution of capelin densities (grams per square metre) varied annually but in general, most capelin occurred in areas where bottom temperatures exceeded 2°C (Fig. 4). In every year except 1984, there were areas where densities of capelin exceeded 100 $g \cdot m^{-2}$ and these areas coincided with relatively warm bottom waters. Densities of capelin plotted against bottom temperatures (Fig. 5) clearly show that high densities of capelin were associated with bottom temperatures greater than 2°C. Low capelin densities were found throughout the range of bottom temperatures measured but high densities occurred only when bottom temperatures exceeded 2°C. The low densities throughout the range of bottom temperatures are not unexpected given the schooling nature of capelin. In addition to capelin, some of these low densities are undoubtedly "biological noise", that is, other species besides capelin that produce an echo return that exceeds the acoustic threshold. In the case of low densities, the species are not always identified because fishing sets were not made. On the other hand, most of the higher densities have been confirmed to be capelin by fishing. In addition, these high densities are likely to be spawning aggregations given that the distribution of recently hatched capelin larvae generally coincides with the distribution of high adult capelin densities. In both 1986 and 1987, the centroids of newly hatched capelin larvae and spawning capelin were less than 37 km apart (Frank et al. 1988; Frank and Carscadden 1989).

The analysis of capelin densities and bottom temperatures using the Cauchy algorithm (Fig. 6) confirms the patterns demonstrated by the horizontal distributions of capelin density. In the ogives, a steep slope along the x axis indicates that only a small range of densities are likely to be observed at this reference temperature, with densities above or below that range unlikely. On the other hand, a shallow slope means that a wide range of densities are possible. While there is some variation in the ogives, in general, the curves are steepest at the lower reference temperatures and slopes are shallower at the higher temperatures. This indicates that at lower temperatures, lower densities of capelin are most probable while at higher temperatures a wide range of densities are likely to occur. The highest densities of capelin will most often occur at the higher temperatures, probably because the capelin are forming dense

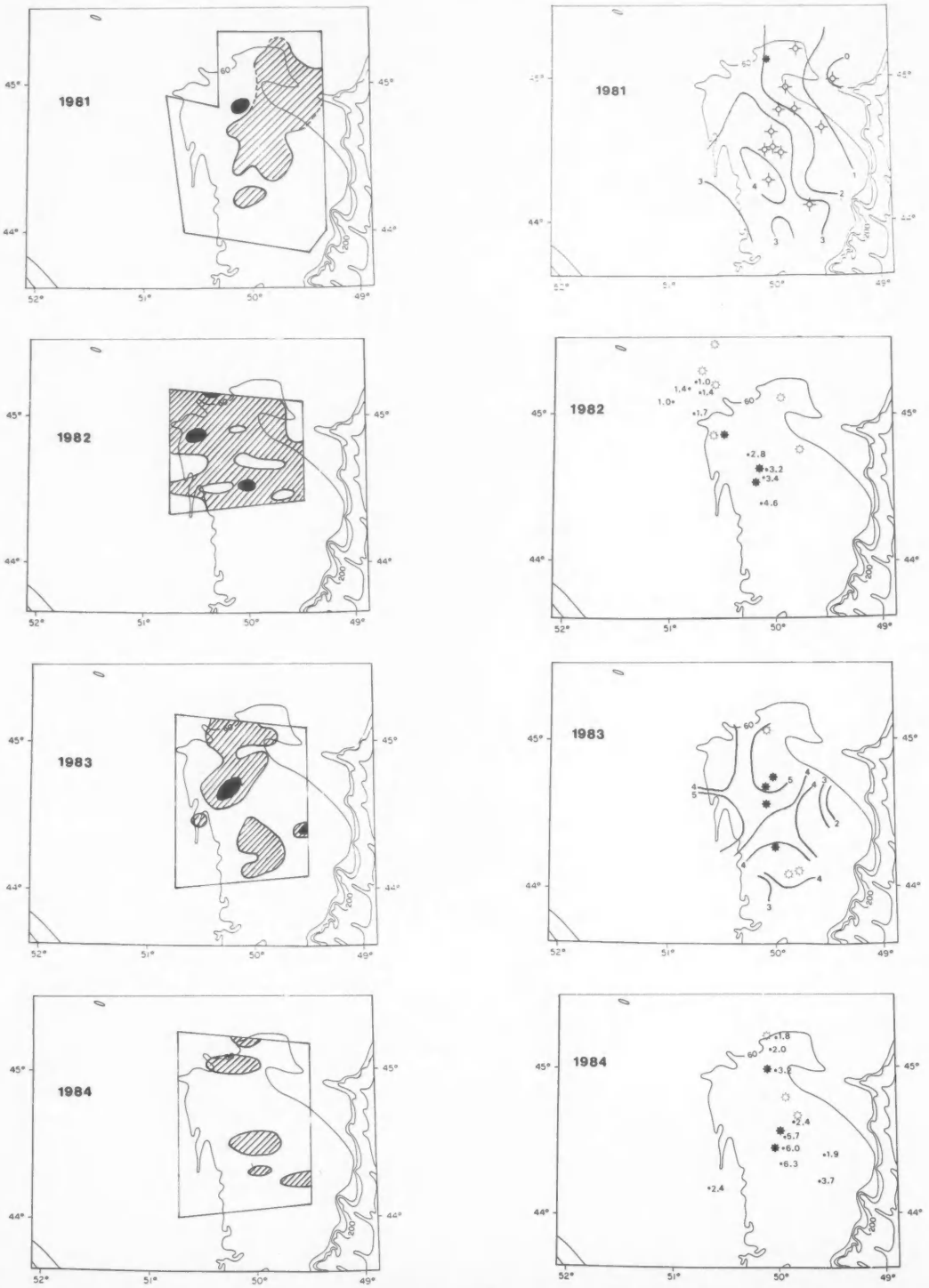

FIG. 4. Densities ($g \cdot m^{-2}$) of capelin from hydroacoustic surveys, bottom temperature (°C) contours during the surveys, and maturities of capelin in fishing sets, 1981–87. Capelin densities: open $<10\ g \cdot m^{-2}$; hatched 10–100 $g \cdot m^{-2}$; solid $>100\ g \cdot m^{-2}$. Temperature: temperature contours not drawn for 1982 and 1984 because of small sample size but actual bottom temperatures are shown. Contours are drawn for 1985 although sample

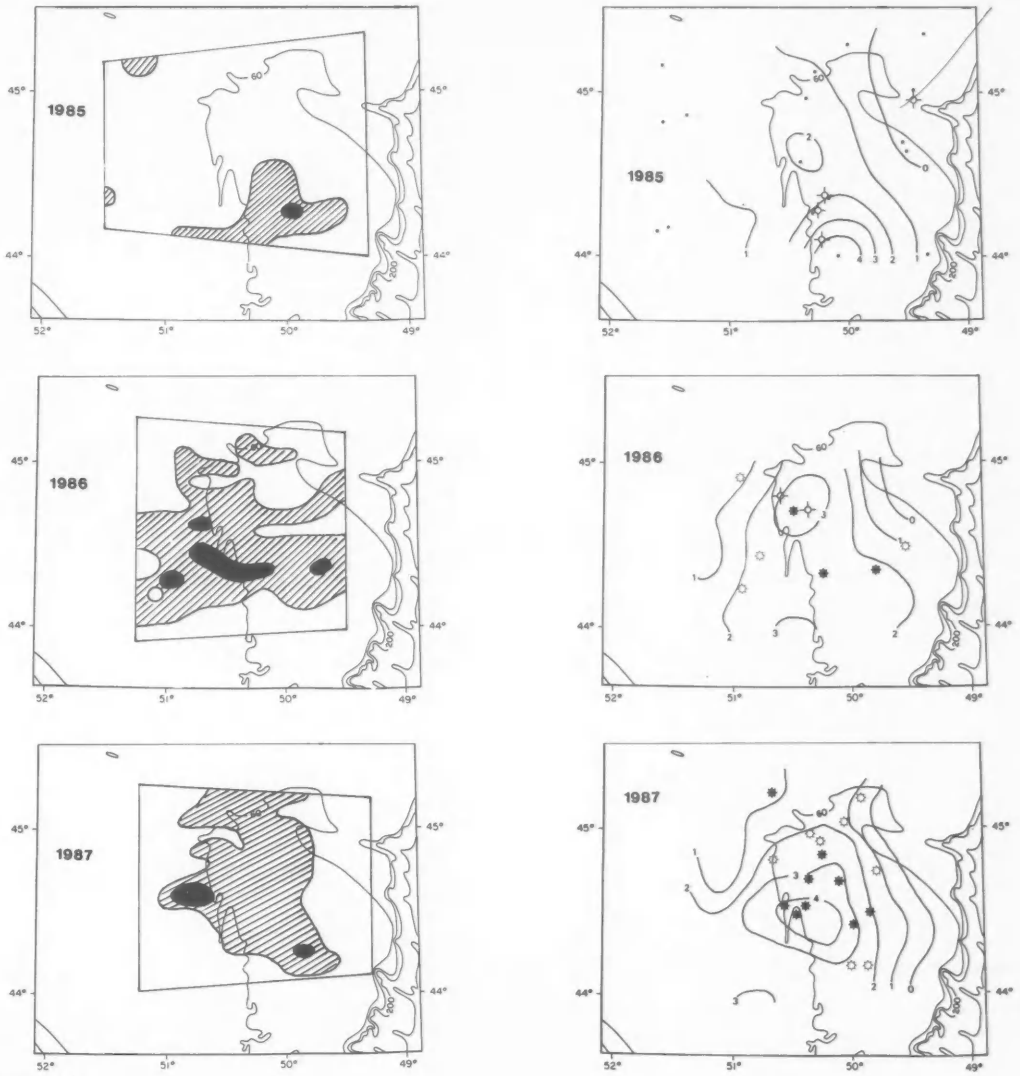

FIG. 4. (*continued*)

sizes are relatively small; and locations of samples are shown by dots (●). Maturities: maturity stage(s) is plotted if it exceeded 50% in the sample. ✧ >50% maturity stage 2 (prespawning); ✹ >50% maturity stage 3 + 4 (imminent spawning and spawning) ✡ >50% maturity stage 5 (spent).

spawning schools. However, this schooling nature also results in instances when low densities occur, even at the higher temperatures. This pattern agrees with divers' observations reported for bottom spawning Barents Sea capelin (Saetre and Gjosaeter 1975). In this area, two types of schools were common. The less dense schools typically were fast moving and probably searched large areas for suitable spawning beds. The dense schools were stationary and very close to spawning.

The overlapping distribution of high densities of mature capelin and bottom water temperatures >2°C and the subsequent larval distributions are good indicators of the relationship between bottom temperatures and spawning on the Southeast Shoal. However, as noted, capelin were encountered throughout the range of water temperatures. This occurrence and the knowledge that capelin exhibit dense aggregations when spawning prompted us to examine the maturity data in detail.

Influence of maturity stage

The maturity data (percent by weight in a fishing set) were superimposed on the bottom temperature distributions (Fig. 4) when the following criteria for the maturity data were met: >50% at maturity stage 2 = maturing, >50% at maturity stages 3 + 4 = imminent spawning and in the act of spawning, or >50% at maturity stage 5 = spent. Using these criteria, there were only two sets, one each in 1981 and 1987, when predominantly spawning fish (stages 3 + 4) occurred where bottom temperatures were less than 2°C. Maturing and spent fish were found throughout the entire range of bottom temperatures from below 0°C to approximately 6°C.

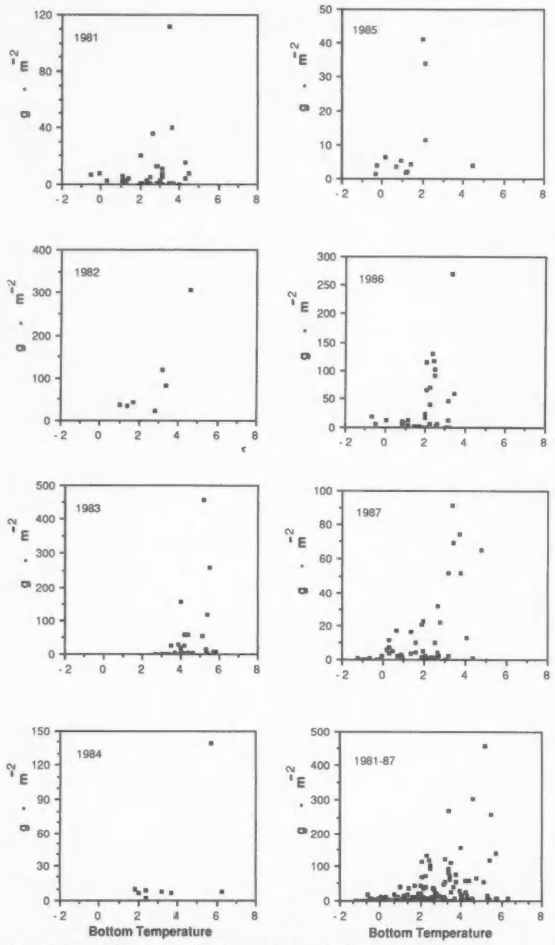

FIG. 5. Densities ($g \cdot m^{-2}$) of capelin in relation to bottom temperatures (°C) on the Southeast Shoal 1981–87 and all years combined.

A composite relationship between each of the five maturity stages and bottom temperatures during the seven annual surveys was constructed (Fig. 7). Low proportions of maturity stages 3 and 4 (i.e. immediately before spawning and during spawning) were found over a wide range of bottom temperatures but higher proportions were almost always encountered at bottom temperatures exceeding 2°C. Fish at maturity stages 1 and 2 occurred over a wide range of bottom temperatures. When high proportions of spent fish (maturity stage 5) were present in the catches, the fish were found at a wide range of bottom temperatures. Our visual impression of the data contained in Fig. 7 was supported by Spearman rank correlation (r_s) analysis of each maturity stage and bottom temperature. The results were as follows:

	Maturity stage				
	1	2	3	4	5
Temperature	−0.34**	−0.13	0.55***	0.43***	−0.19

A similar analysis of the maturity stages with depth revealed only one significant relationship (stage 4: $r_s = -0.36$, $p < 0.05$).

Discussion

Our analysis indicates that the incidence of mature capelin on the Southeast Shoal during late June and July is a predictable occurrence and that the densest concentrations most often occur where bottom temperatures exceed 2°C. The maturity data show that immature, maturing, and spent capelin are likely to be found over a wide range of water temperatures and that it is more probable that spawning capelin will be found in the warmest bottom temperatures. While there is annual variation in the distribution of the densest concentrations of capelin, the centroids are concentrated in a relatively small area (Fig. 2), given both the magnitude of the spawning migration to the Southeast Shoal and the overall size of the Grand Banks possessing other suitable spawning substrate. The final selection of spawning site(s) is affected by bottom temperature with approximately 2°C representing a minimum threshold. These results are consistent with our original hypothesis, namely that the ultimate influence on spawning location for Southeast Shoal capelin is suitable substrate, the origin of which was determined by the geological history of the Grand Banks, and that the proximate influence on the final spawning location, within the Southeast Shoal area, is bottom water temperature.

Studies on Barents Sea capelin support our observations on the influence of water temperature (Ozhigin and Luka 1985; Tjelmeland 1987), although these studies are more general in nature and do not provide detailed information on maturity and temperature. During years of warm water temperatures in the Barents Sea, capelin spawned more to the east on the Norwegian–USSR coast than in cold years (Ozhigin and Luka 1985). Tjelmeland (1987) analyzed capelin distribution data many months prior to spawning and found a positive correlation between east–west migration and the autumn temperature gradient, during the prespawning migration. On the other hand, he found a negative correlation between east–west migration and the spring temperature gradient which is consistent with the theory that capelin seek a relatively warm or at least optimal temperature during the month prior to spawning.

While our study deals with spawning conditions for capelin on the Southeast Shoal, specifically substrate and bottom temperature conditions, it is obvious that other environmental conditions in the area are suitable for long-term viability of the population. For instance, some environmental factors affecting larval capelin survival on the Southeast Shoal have been identified by Frank et al. (1988) and Frank and Carscadden (1989). This area seems to be a zone of high primary productivity; high chlorophyll concentrations were recorded in the northern part of the Southeast Shoal and the shelfbreak (Anderson and Gardner 1986) confirming other reports (Mobil Oil Ltd., unpubl. data; reported in Anderson and Gardner (1986)) of enhanced phytoplankton biomass and production in the Southeast Shoal area. As previously noted, there are other areas on the Grand Banks, based on sediment structure alone, that would appear to be suitable for capelin spawning. Indeed, Pitt (1958) reported four instances during 1948 and 1949 where ripe or spent capelin were found on offshore banks (other than the Southeast Shoal) in the Newfoundland area and concluded that capelin spawn at various places on the offshore banks. However, in spite of extensive research vessel surveys and large commercial fisheries in the intervening years, there have been no reports of capelin spawning offshore, except on the Southeast Shoal. This prompts the question of why there are no other bottom spawning capelin populations on the Grand Banks; to address ths

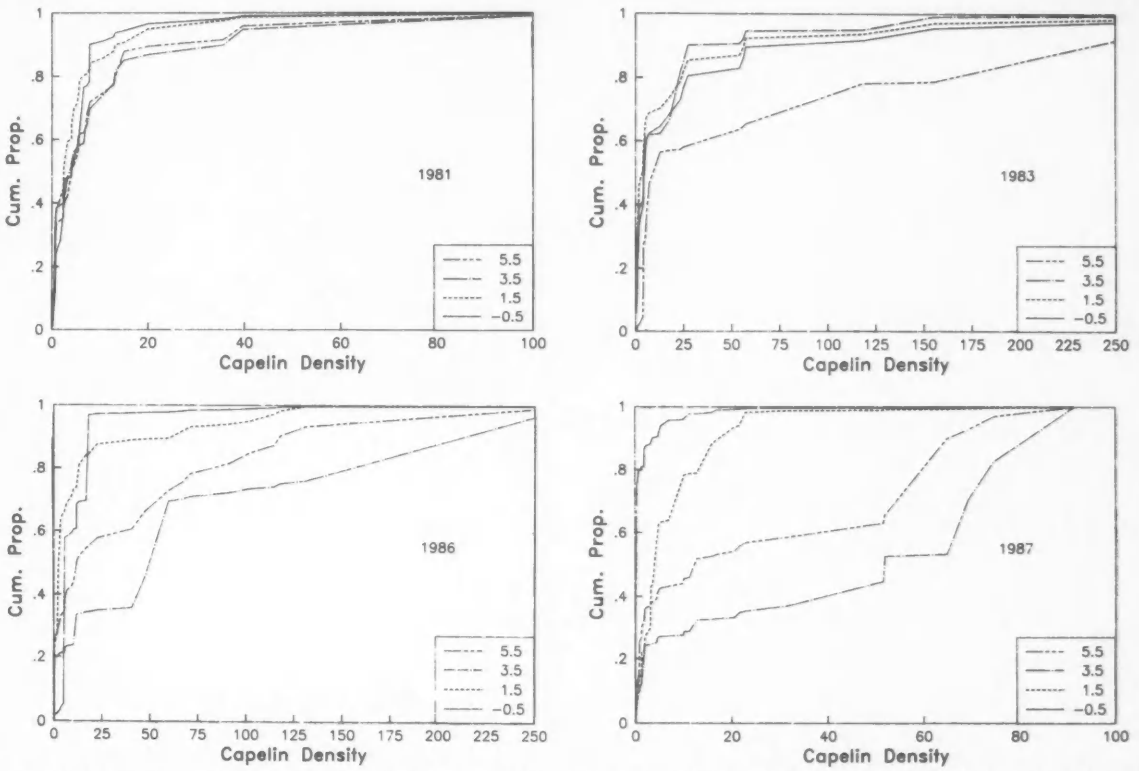

FIG. 6. Probability density functions of capelin density at four reference temperatures (−0.5, 1.5, 3.5, and 5.5°C) for 1981, 1983, 1986, and 1987.

question we examined data relating to factors known to affect spawning, egg development, and larval survival.

We have shown that the minimum threshold bottom temperature for capelin spawning is approximately 2°C. Monthly means of temperature for selected subareas (Fig. 8) of the Grand Banks (Drinkwater and Trites 1986) at 75-m and 100-m depths (representing near bottom temperatures in different areas) were examined. We chose subareas on the Grand Banks (subarea 17, 18, 19, 20, and 22) exhibiting suitable spawning substrate (Fig. 2) and a subarea encompassing St. Pierre Bank (subarea 33) because Pitt (1958) reported that capelin probably spawned there. The long-term monthly means at both depths (Fig. 8) indicate that temperatures barely exceed 2°C during June and July in only one area, subarea 22, west of the Southeast Shoal.

Bottom temperatures after July in most areas rarely exceed 1–2°C and although capelin eggs can survive at these low temperature (Davenport and Stene 1986), a prolonged development time would occur. Frank and Leggett (1981) reported median hatching times of beach-spawned eggs were determined by average daily incubation temperatures and the relationship they derived was indistinguishable from one using data from a series of experiments conducted by Jeffers (1931); Sleggs (1933); and Fridgeirsson (1976). Using the Frank and Leggett (1981) relationship, hatching at 0 and 1°C would take 72 and 46 d, respectively. On the other hand, hatching at 3–5°C, typical of temperatures on the Southeast Shoal, would take 30 to 23 d. Thus, depending on the actual bottom water temperatures in other potential spawning locations on the Grand Banks, hatching could take two to three times longer than on the Southeast Shoal. This would not only make the eggs more vulnerable to predation during an extended incubation period but delayed hatching would put these larvae at a selective disadvantage in terms of feeding, growth, predator avoidance and overwintering survival potential (e.g. Oliver et al. 1979; MacLean et al. 1981).

Newly hatched capelin larvae in the offshore areas must move from the sea bottom to the surface to find food. Frank and Carscadden (1989) presented a hypothesis and supporting data on a possible mechanism used by capelin to overcome this problem. Their hypothesis draws on the knowledge of beach-spawned capelin where it has been shown that sharp increases in water temperature coupled with wave turbulence are the environmental signals that trigger emergence and drift of larvae (Leggett et al. 1984). During 1986, the formation of the dominant larval cohort on the Southeast Shoal coincided with a storm event and sharp increases in both bottom currents and bottom temperatures, which reflected an episode of destratification due to in situ mixing. A second cohort, produced in the absence of any abrupt change in the physical environment, did not fare as well (Frank and Carscadden 1989). Similar larval and hydrographic collections were made in 1987 and larval abundances were one to two orders of magnitude lower than in 1986 with no dominant cohorts beyond the post-yolk-sac stage. There were no significant storm events in 1987 although there was a large tongue of warm, salty subsurface water covering the study area. Frank and Carscadden (1989) suggested that the presence of these slope water intrusions may not be as effective

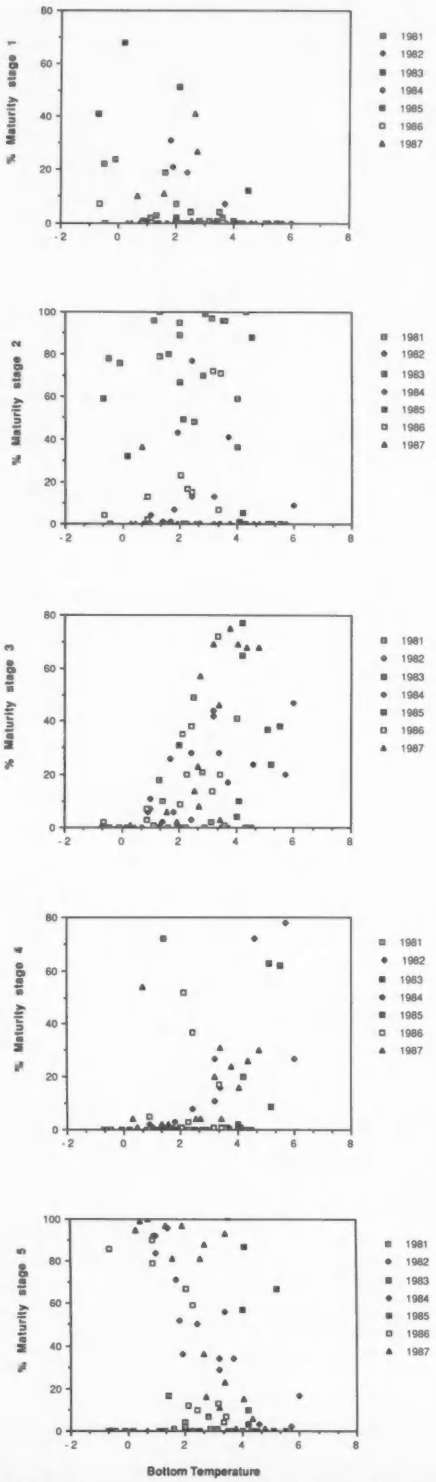

FIG. 7. Maturity stages (%) of capelin in relation to bottom temperature (°C) 1981–87.

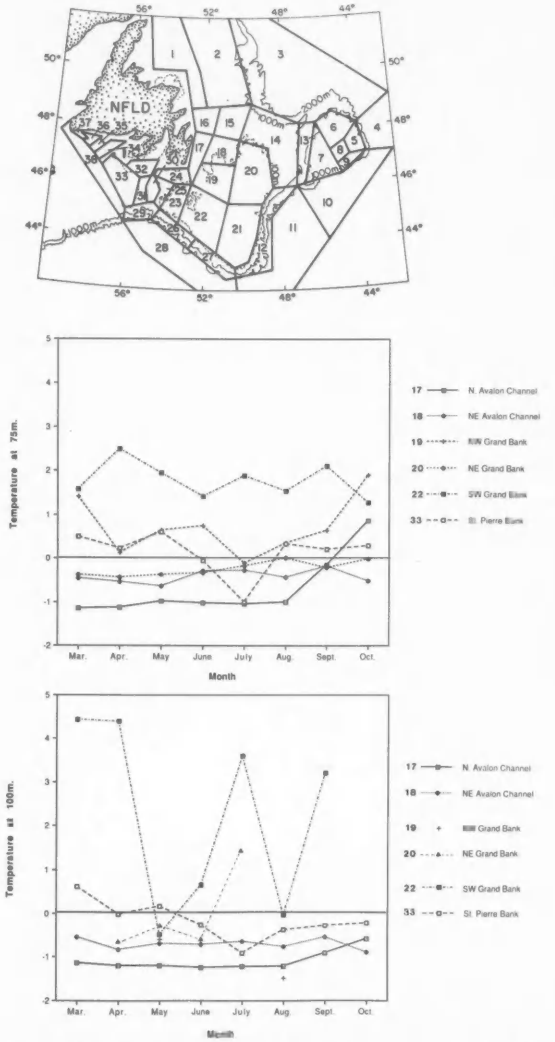

FIG. 8. Monthly temperatures (°C) at 75 m (middle panel) and 100 m (bottom panel) from subareas shown in top panel (from Drinkwater and Trites 1986).

TABLE 2. Maximum speeds (cm/s) of the horizontal oscillatory bottom currents likely to be induced by surface waves, at different wave periods (Ts in s) and depths (m). The wave amplitude in this calculation was (= 1/2 wave height) 1 m. From Harden Jones and Scholes (1980).

	Wave period Ts					
Depth	6	7	8	9	10	11
30	7	15	22	29	34	38
40	2	7	12	18	23	28
50	1	3	7	11	16	20
60		1	4	7	11	15
70		1	2	4	7	11
80			1	3	5	8
90			1	2	3	6
100				1	2	4

at triggering larval release as in situ mixing generated by storms which would produce both a thermal signal and bottom turbulence.

Frank and Carscadden (1989) estimated that erosion velocities of about 15 cm/s were required to move sand (0.25–0.5 mm in diameter); the erosion velocities would have to be greater for larger grain sizes. Using available wave data for the Southeast Shoal, maximum speeds calculated were occasionally sufficient ($\geq$ 20 cm/s) to cause erosion at 50 m and therefore could trigger larval emergence. Bottom currents increase with wave period at a given wave height but decrease with depth (Table 2). Thus, at the largest wave period (11 s), bottom currents decrease by a factor of five between 50 (Southeast Shoal) and 100 m (other areas of the Grand Banks). Even sand grains would not be eroded at depths greater than 70 m. Using 11-yr wave statistics for Hibernia (approximately 46°45′N, 48°47′W), 92% of the wave observations occurred with periods less than 12 s and wave heights less than 5 m. Of 8036 observations most occurred in the 2–4 m height range and 6–8 s range (Neu 1987). The relationship between wave height, wave period, water depth, bottom current velocity (see Harden Jones and Scholes 1980 for formulae and Frank and Carscadden 1989) and size of particle eroded is not simple and we cannot unequivocally state that bottom substrate will never be eroded over deeper areas of the Grand Banks. However, given the trends illustrated in Table 2 and the observations of wave height and period for the Grand Banks (Neu 1987), it is obvious that the probability of erosion occurring on the Southeast Shoal as a result of wind events is significantly greater than at greater water depths in all other regions of the Grand Banks. Similarly, the likelihood of thermal destratification due to storm passage is greater on the Southeast Shoal than other areas of the Grand Banks.

It is highly improbable that the appropriate combination of the environmental factors known to influence capelin spawning, egg development time, and release of larvae from the sediment would occur simultaneously over the long-term over most of the Grand Banks. The only area where these characteristics occur is the Southeast Shoal. We reiterate our original suggestion that this population was once a beach-spawning population but became adapted to spawning in water depths of about 50 m with the rise in sea level coincident with glacier melt. Substrate and bottom temperatures are suitable for spawning and environmental factors subsequent to spawning are favourable to promote the long-term viability of the population.

The Southeast Shoal also supports unique populations of two species of bivalves. Nesis (1965) reported a high biomass of the bivalve mollusc *Mesodesma arctatum*, the wedge clam, and stated that such a high biomass so far from a coast is extremely rare. A population of large *Mytilus edulis*, the blue mussel, is one of the world's few sublittoral populations and the farthest one from shore. These two species co-occurred with *Cucumaria frondosa*, the sea cucumber, and this species grouping (''biocoenosis'') does not have a counterpart anywhere in the world (Nesis 1965). It is quite probable that the original occurrence and persistence of the two sublittoral species in the Southeast Shoal region is linked to its geological history and to the unique environmental features to which they are adapted, in a manner parallel to that of capelin.

Acknowledgments

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Accumulation of Essential and Nonessential Metals by Chironomid Larvae in Relation to Physical and Chemical Properties of the Elements

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Krantzberg, G. 1989. Accumulation of essential and nonessential metals by chironomid larvae in relation to physical and chemical properties of the elements. Can. J. Fish. Aquat. Sci. 46: 1755–1761.

Molar concentration factors for nine metals, calculated as quotients of concentrations in chironomids divided by concentrations in sediment, were systematically related to fundamental atomic properties using multiple regressions and canonical analyses. Ionization and oxidation potentials, as well as the ionization potential differential and atomic radius, were useful predictors of metal concentration factors. Their relative importance varied with lake pH. Concentration factors were higher for the essential elements Zn, Ca, and Cu than for Ni and the nonessential elements Pb, Cd, and Al. The low concentration factors for Mn and Fe were driven by high sediment concentrations and the tendency for these elements to form insoluble hydroxides.

Les facteurs de concentration molaire pour neufs métaux, calculés comme étant le rapport des concentrations dans les chironomidés sur les concentrations dans les sédiments, ont été liés de façon systématique aux propriétés atomiques de base à partir de régressions multiples et d'analyses canoniques. Les potentiels d'oxydation et d'ionisation, ainsi que le potentiel différentiel d'ionisation et le rayon atomique ont été des utiles caractéristiques de prédictions des facteurs de concentration des métaux. L'importance relative de ces caractéristiques a varié en fonction du pH du lac. Les facteurs de concentration étaient plus élevés dans le cas des éléments essentiels Zn, Ca et Cu que pour le Ni et les éléments non essentiels Pb, Cd, et Al. Les faibles facteurs de concentration trouvés pour le Mn et le Fe étaient liés à des concentrations élevées dans les sédiments et à la tendance pour ces éléments à former des hydroxydes insolubles.

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In sediments, metal bioavailability is a function of the physicochemistry of the sediment–water system (Gambrell et al. 1976; Luoma and Bryan 1978; Apts 1980; Forstner and Wittmann 1981; Prosi 1981; Winner 1984) and the chemical properties of a particular metal. The importance of pH in determining metal bioavailability has been well documented (Stokes and Cambell 1987). Factors that affect the affinity of a metal for biological tissues will also depend upon the chemical properties of that element or the reactivity of the metal with various ligands (Tessier et al. 1984). Kaiser (1980) was able to relate toxicity to elemental characteristics, including electron configuration, ionization potential, atomic number, and ionic radius. Lemons and Kennington (1983) provided evidence that descrimination or bioaccumulation of nonessential metals was partially dependent upon their chemical similarity to essential metals. Irrespective of these kinds of observations on metal bioaccumulation, few studies have attempted to synthesize information on metals in the biota, with bioavailability, and the chemical properties of the elments.

Since the electron configuration, ionization potential, and atomic radius strongly influence the preference for and stability of metal–protein complexes, these properties might correlate with the uptake of metals from sediment by benthic organisms. In this paper, I use multiple linear regression and canonical correlation analysis to identify the important elemental and environmental characteristics influencing concentrations factors for nine metals in chironomid larvae from eight softwater lakes.

Materials and Methods

Study Sites

Chironomids and sediment were collected from eight lakes in two geograpical regions in the springs of 1984, 1985, and 1986. The lakes differed in pH and concentrations of metals. In the Muskoka–Haliburton region of south central Ontario, four lakes were sampled and pH ranged from 5.4 to 6.3 (Table 1). In the Wanapetei region of central Ontario, four lakes were sampled and pH ranged from 4.4 to 5.3.

Field Collections

Chironomid larvae and sediment were collected by Ekman grab or gravity corer from 1 to 15 m depth at two or three sites per lake. At each site, a minimum of 20 grab samples were sieved through a 200 or 500-μm Nytex nylon mesh to remove

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TABLE 1. Physical and chemical characteristics of study lakes. (A = area, Z = mean depth, Z_{max} = maximum depth, cond = conductivity, TP = total P, TN = total N, DOC = dissolved organic C, Secchi = secchi depth, %LOI = percent lost on ignition). Data provided by the Ontario Ministry of the Environment and the Canadian Wildlife Service.

Lake	A (ha)	Z (m)	Z_{max} (m)	pH	Cond ($\mu S \cdot cm^{-1}$)	Ca ($mg \cdot L^{-1}$)	TP ($\mu g \cdot g^{-1}$)	TN ($\mu g \cdot g^{-1}$)	DOC ($mg \cdot L^{-1}$)	Secchi (m)	% LOI
Muskoka–Haliburton											
Plastic	32	8.0	16.0	5.4	23	1.9	4	155	2.4	6.2	42
Crosson	57	8.4	25.0	5.6	25	2.2	8	208	5.2	3.7	32
Red Chalk	57	14.2	38.0	6.3	22	2.5	5	155	3.9	6.0	44
Heney	22	3.3	6.0	5.8	24	1.9	7	210	2.9	4.6	36
Gullfeather	66	4.8	12.0	5.8	27	2.1	11	250	6.9	2.5	49
Wanapetei											
240	15	8.5	14.0	5.1	27	2.2	7	179	1.4	6.8	47
401	3	3.0	3.6	4.4	41	1.7	5	300	4.4	2.1	55
402	9	6.5	8.5	4.4	41	2.0	6	200	3.5	6.5	51
403	10	4.3	4.4	4.4	43	1.6	5	200	1.0	4.3	53
404	7	6.1	7.6	5.0	31	2.8	5	227	0.1	5.0	43
408	8	1.7	2.0	4.4	46	1.6	5	200	5.1	1.6	58

chironomids. Larvae were placed in plastic bags containing lake water with a small amount of sediment and were kept cool for no more than 24 h until proceeding with laboratory analysis. Sediment for metal analysis were sealed in plastic bags and held at 4°C for no more than 2 wk until processing.

Sample Preparation and Analysis

In the laboratory, chironomids were sieved from sediments through a 200-μm Nytex nylon mesh and placed in lake water for 24 h to eliminate gut contents. Water was changed three times to reduce coprophagy. Pooled samples of fourth instar larvae (approximately 50 individuals) were dried to constant weight at 60°C, placed in Erlenmeyer flasks, digested to dryness with hot HNO_3 and resuspended in dilute HNO_3. Suspensions were filtered through acid-washed Whatman filter papers (Black Ribbon) and brought to 10 mL final volume with distilled water. All plastic and glassware were acid-washed in 7% NHO_3 for 24 h. and rinsed in seven changes of distilled water. Aluminum, Ca, Cu, Fe, Mn, Ni, and Zn were analyzed using an ARL 34000 Inductively Coupled Plasma Argon Emission Spectrophotometer and Pb and Cd were determined by an Scintrex Zeeman-Modulated Tungsten Filament Atomic Absorption Spectrophotometer (AAZ-2). National Bureau of Standards (NBS) oyster tissue and National Research Council of Canada (NRCC) lobster hepatopancreas were analyzed as checks on the accuracy of the methods. Recoveries were within 7% of certified values. Standards were run every eight to 12 samples to confirm the reproducibility of the measurements.

Wet sediment was partitioned into two size fractions: whole sediment (<0.5 mm) and sediment that could pass through a 67-μm nylon mesh. The latter fraction was used as an approximation of ingestible sediment following a preliminary analysis of gut contents which revealed the absence of particles greater than 67 μm in the foregut. Two size classes were retained for examination based, as well, on the differential metal binding capacities of small and large sediment particles (Filipek and Owen 1979; Ackerman 1980; Thorne and Nickless 1981; Forstner and Salomons 1980; Forstner 1982). Total metal concentrations in dry sediment and National Bureau of Standards river sediment were determined by extraction in concentrated NHO_3:$HC10_4$ (2:1, v:v), at 150°C and an acid to sediment ratio of 20:1 (v:v). Metals were analyzed by ICP and AAS. Recoveries were within 7% of certified values.

For each metal, tissue concentrations were calculated for whole body, adsorbed, and internally incorporated metals. The latter two values were estimated from measurements reported by Krantzberg and Stokes (1988). For each tissue, concentration factors (*CF*) were calculated based on metal concentrations in whole and sieved sediment:

$$CF_i = M_{ij} / M_{ik},$$

where M_{ij} is the metal concentration in nanomoles per milligram dry weight (i = Al, Ca, . . .Pb) for a specific tissue (j = whole body, internal, or adsorbed). M_{ik} is the metal concentration in nanomoles per milligram dry weight for a specific sediment fraction (k = whole or sieved). For the purposes of the discussion, the following nomenclature will be adopted:
whole/whole: *CF* for whole-body concentration versus metal concentration in whole sediment;
internal/whole: *CF* for internal metal concentration versus metal concentration in whole sediment;
adsorbed/whole: *CF* adsorbed metal concentration versus concentration in whole sediment;
whole/sieved: *CF* for whole-body concentration versus metal concentration in the sieved sediment;
internal/sieved: *CF* for internal metal concentration versus metal concentration in the sieved sediment;
adsorbed/sieved: *CF* for adsorbed metal concentration versus metal concentration in the sieved sediment.

For each metal, six concentration factors were calculated (three tissues × two sediment fractions) for each of the pooled chironomid samples (n = 3–10) at each site (n = 19 sites, Fig. 1). A total of 146 chironomid samples and sediment samples were analyzed to produce the concentration factors. These concentration factors were correlated with ionization potential, ionization potential differential (IPD, the difference in ionization potential at the next lower oxidation number), oxidation potential, atomic radius, atomic number (AN), and the log of AN/IPD. Values for these parameters were obtained from Fine (1972) and Kaiser (1980) (Table 2).

Statistical Analyses

Two statistical techniques were used to identify the elemental properties that were correlated with the concentration factors.

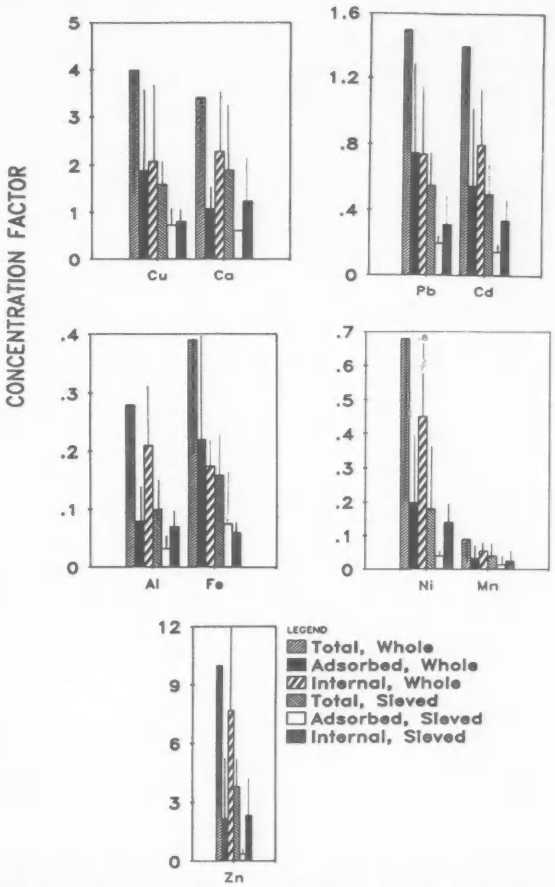

FIG. 1. Mean concentration factors for chironomids, calculated on the basis of whole body, adsorbed, or internal concentrations (nmole·g^{-1} dry weight), versus concentrations in whole (<200 μm) or sieved (<67 μm) sediments (nmole·g^{-1} dry weight). Histograms represent mean values for all samples, vertical bars are standard deviations (n = 146 pooled chironomid samples and 146 sediment samples).

Stepwise multiple regressions were used to identify the minimum number of independent variables that explained the variance in concentration factors. Due to the sensitivity of this technique to the sequence in which variable are entered, canonical correlations were also performed to evaluate the hypotheses generated by the multiple regressions. Multiple regression finds the maximum correlation between linear functions of two sets of variables (Blackith and Reyment 1971). Canonical correlation allows an additional examination of the interdependencies between two sets of data, but is sensitive to the heuristic interpretation of the end products.

Stepwise multiple regressions based on a forward variable entry protocol were used to examine the correlation of elemental properties with metal concentration factors (Steel and Torrie 1960). The forward variable entry procedure calculated the F-statistic for each of the properties and the property with the highest F-statistic was entered. F-values were recalculated for the remaining properties and additional properties were added to the model until the F-value was below that which was specificed. Properties added to the model were not removed. An F-value >5.0 at $p<0.05$ was selected as the decision criterion for adding properties. Correlations were calculated by lake pH (two lakes each at pH 4.4, 5.1, 5.5, and 6.0), and for the whole data set. In order to avoid pseudoreplication with respect to lake pH, lakes of pH 5.8 and 6.3 were both considered to be at 6.0. Such data treatment seems realistic as pH 6.0 was within one standard deviation of the mean pH for both lakes.

Canonical correlation analyses were also used to compare the concentration factors with the elemental properties. A canonical correlation between the six concentration factors and the six elemental properties was conducted, using correlation matrices, for the whole data set in order to further examine the interrelation between the affinity of metals for biological tissues and their relative physical and chemical characteristics. Statgraphic software was employed (STSC 1985).

Results

pH 4.4 Sites

The greatest amount of variability in *CF*'s was explained in the correlation of internal/whole *CF*'s on the elemental properties, followed by internal/sieved and whole/whole (Table 3). For internal/whole *CF*'s versus the elemental properties, oxidation potential accounted for the most variation and was negatively correlated with ionization potential (Table 5). For the suite of metals considered, oxidation potential was highest for Ca, followed by Al, Mn, and Zn. Concentration factors of Ca and Zn were greater than those of the other elements (Fig. 1). Ionization potential positively influenced *CF*'s and was negatively correlated with oxidation potential. Log AN/IPD negatively influenced *CF*'s and was positively correlated with atomic number. Lead and Cd, for example, have relatively high ionization potentials and their relatively high Log (AN/IPD and/or atomic number were reflected by *CF*'s that were lower than those of Ca and Zn. The contribution of oxidation potential to the model might also reflect the negative correlation between ionization potential differential and oxidation potential.

Atomic radius explained the most variation in the internal/sieved *CF*'s followed by Log AN/IPD (Table 3). Atomic radius was positively correlated with oxidation potential, ionization potential, and ionization potential differential, and might have acted as a surrogate from them in the multiple regression. Lead and Cd *CF*'s were lower than would be predicted on the basis of atomic radius (or oxidation potential) alone. This result may be a consequence of their high values for Log AN/IPD. Both adsorbed/whole and adsorbed/sieved *CF*'s were negatively correlated with oxidation potential and weakly positively correlated with atomic radius. This combination of elemental properties best characterizes Ca, which also had the highest *CF* for adsorbed metal. For all metals and all body tissues, *CF*'s were greater for whole sediment than for sieved sediment, reflecting the higher metal concentration in the <67 μm fraction.

pH 5.1 Sites

For both internal/sieved and internal/whole *CF*'s, 97% of the variation was explained by the multiple regressions of *CF*'s against elemental properties. Ionization potential was most important in explaining the variability in *CF*'s, followed by a negative contribution by ionization potential differential and a positive contribution by oxidation potential (Table 3). Given that ionization potential differential and oxidation potential were

TABLE 2. Atomic properties of some essential and nonessential metals. eV = electron volts, A = Angstroms. Letters in parentheses are codes used in the text. Values are from Fine (1972) and Kaiser (1980).

Metal	Electron configuration	Ionization potential eV (IP)	Atomic radius A (AR)	Atomic number (AN)	Oxidation potential eV (OP)	Ionization potential differential eV (IPD)	Log AN/IPD
Aluminum	$3s^2\ 3p^1$	5.97	1.54	13	1.71	9.62	6.07
Calcium	$4s^2$	6.11	1.97	20	2.76	5.76	3.47
Manganese	$3d^5\ 4s^2$	7.43	1.17	25	1.03	8.21	3.04
Iron	$3d^6\ 4s^2$	7.83	1.16	26	0.41	8.28	3.14
Nickel	$3d^8\ 4s^2$	7.61	1.15	28	0.23	10.52	2.66
Copper	$3d^{10}\ 4s^2$	7.72	1.17	29	0.16	12.57	2.31
Zinc	$3d^{10}\ 4s^2$	9.39	1.25	30	0.76	8.57	3.50
Cadmium	$4d^{10}\ 5s^2$	8.99	1.41	48	0.40	7.91	6.07
Lead	$6s^2\ 6p^2$	7.38	1.54	82	0.28	10.38	7.90

negatively correlated, the magnitude of variation explained by each factor in the model may not represent the actual significance of each of the elemental properties. A significant but small amount of variation was also related positively to atomic number and negatively to Log AN/IPD.

Zinc had the highest internal/whole and internal/sieved *CF*'s followed by Cu, Pb, and Cd, respectively, with Ca holding a variable position depending upon the sediment type (Table 3). Concentration factors for the remaining elements were <0.10.

Oxidation potential, ionization potential differential, ionization potential, and Log AN/IPD explained 88–92% of the variation in whole body *CF*, with the relative importance of each variable differing between sediment types. For *CF*'s based on adsorbed metal, oxidation potential was the most important elemental characteristic and was positively correlated with the *CF*. It is possible that atomic radius may also have been important in determining metal *CF*'s, but was not entered into the regression due to its correlation with oxidation potential. Ionization potential differential was next important in explaining variability, but was negatively associated with the *CF*'s. The negative correlation between oxidation potential and ionization potential differential further suggests that these two elemental characteristics operate in an opposing manner in the establishment of metal burdens. Due to the correlation between these two properties, however, the absolute importance of each one in determining metal accumulation was not discernible.

pH 5.5 Sites

For organisms from the pH 5.5 sites, *CF*'s were most poorly related to the elemental properties examined, with r^2 values not exceeding 0.62. The ionization potential, ionization potential differential, and oxidation potential were important factors in explaining all *CF*'s. The *CF*'s for all tissue:sediment combinations decreased in the sequence Zn>Cu>Ca>Ni>Cd (Fig. 1). The *CF*'s of Zn, Cu, Ca, Ni, and Cd were >1 for whole sediments, but were <1 for Ni and Cd in the <67-μm fraction. Atomic radius may also have influenced metal accumulation but was not included in the regression due to its positive correlation with oxidation potential.

pH 6.0 Sites

The *CF*'s based on sieved sediment were better related to the elemental properties than were those based on whole sediment. The ionization potential differential, ionization potential, and oxidation potential explained 87% of the variation in whole/sieved *CF*'s, and 79% of the variation in internal/sieved *CF*'s. The oxidation potential and ionization potential were positively related to whole sediment *CF*'s, but their relative importance changed among tissues (Table 3). A negative relationship emerged between Log AN/IPD and whole/whole *CF*'s, but Log AN/IPD was not significantly related to adsorbed or internal tissue *CF*'s. The highest *CF*'s for all sites were observed for the pH 6.1 lakes, with *CF*'s for Zn, Cu, Ca, Pb, and Cd being 16, 5, 4, 2, and 2, respectively.

Canonical Correlation

The coefficients for the first canonical variate of the *CF*'s were negative for those based on whole sediment, particularly for adsorbed metal *CF*'s. The coefficients were positive for those based on whole sediment, with especially high loadings in internal/sieved *CF*'s (Table 4). This variate, then, was interpreted as representing *CF*'s that were calculated on the basis of organism concentrations, particularly of internal tissues, versus the <67 μm sediment fraction. The corresponding canonical variate for the six elemental properties had positive loadings for ionization potential, ionization potential differential, atomic radius, and a particularly high coefficient for oxidation potential. Log AN/IPD had a negative coefficient. This variate, then, can be considered as one that had low loadings for elements with very high Log AN/IPD values, such as Pb and Cd, and with very low ionization potentials, such as Al. It had the highest coefficients for the essential elements Ca, Zn, Ni, and Cu, all of which have relatively high values for at least one of the positively loaded characteristics, and low scores for Log AN/IPD. The correlation between these vectors and the *CF*'s was 0.82 and explained 67% of the variability between the data sets.

The second canonical variate had a positive coefficient for adsorbed/sieved *CF*'s and an even higher positive coefficient for adsorbed/whole *CF*'s. All the remaining coefficients were negative. This variate had highest scores for sites with high concentrations of adsorbed metals relative to those of whole sediment. The positive loading for sieved sediment is probably a consequence of the positive correlation between sieved and whole sediment concentration factors. The second canonical variate for the elemental characters had positive coefficients for ionization potential differential and atomic radius and negative coefficients for oxidation potential. High values for this variate are representative of Pb, and to a lesser extent, Cu

TABLE 3. Relative contribution of the elemental properties to the total amount of variation explained by stepwise multiple regression of metal concentration factors against elemental properties.

Lake pH = 4.4	R^2	Internal > versus whole .94	Internal versus sieved .83	Whole > versus whole .83	Whole > versus sieved .80	Adsorbed > versus sieved .72	Adsorbed versus whole .68
				Percent of variation explained			
Ionization potential		14	1	7	0	0	10
Oxidation potential		43	0	46	57	48[a]	20[a]
Ionization potential differential		13[a]	0	7[a]	11[a]	4[a]	18[a]
Atomic radius		4	51	7	0	14	13
Log (AN/IPD)[b]		16[a]	17[a]	2[a]	6[a]	0	7[a]
Atomic number		3	10	13	0	4	0

Lake pH = 5.1	R^2	Internal versus sieved .97	Internal > versus whole .97	Whole > versus sieved .92	Whole > versus whole .88	Adsorbed versus sieved .70	Adsorbed versus whole .70
Ionization potential		32	37	23	29	3	9
Oxidation potential		22	18	29	23	39	30
Ionization potential differential		24[a]	22[a]	26[a]	0	21[a]	22[a]
Atomic radius		0	0	0	0	3	2
Log AN/IPD		15[a]	17[a]	12[a]	35[a]	4[a]	7[a]
Atomic number		3	3	1	0	0	0

Lake pH = 5.5	R^2	Internal versus whole .62	Whole > versus whole .62	Whole versus sieved .60	Internal versus sieved .60	Adsorbed versus sieved .60	Adsorbed versus whole .60
Ionization potential		15	14	14	15	10	8
Oxidation potential		13	26	15	19	5	0
Ionization potential differential		35	42	31	26	44	49
Atomic radius		0	0	0	0	0	2

Lake pH = 6.0	R^2	Whole > versus sieved .87	Internal > versus sieved .79	Adsorbed > versus sieved .74	Whole > versus whole .69	Adsorbed > versus whole .63	Internal versus whole .58
Ionization potential		23	20	17	21	24	18
Oxidation potential		14	29	54	17	47	25
Ionization potential differential		46	29	2	0	31	15
Log AN/IPD		5[a]	0	0	30[a]	0	0
Atomic number		0	0	0	0	4	0

[a]Negative correlation with concentration factor.
[b]See text for explanation.

TABLE 4. Coefficients for the first two canonical variables of the correlation between metal concentration factors and elemental properties. VAR. 1 and VAR. 2 refer to the first and second significant canonical variables, respectively. (see text for an explanation of the concentration factors and elemental properties).

	Coefficients for canonical variables				
	Concentration factor			Elemental property	
	VAR. 1	VAR. 2		VAR. 1	VAR. 2
Whole/whole	−0.9892	−2.7275	IP[a]	1.7420	0.3138
Internal, whole	−2.9870	−0.1502	OP[b]	2.1052	−0.7773
Adsorbed, whole	−0.1714	3.5237	IPD[c]	0.8040	1.0349
Whole, sieved	1.6654	−0.5047	AR[d]	−0.0374	1.3379
Internal, sieved	1.2572	−0.7200	AN[e]	0.8358	−0.3423
Adsorbed, sieved	2.1544	1.2721	LOG[f]	−0.7069	0.0671

[a]Ionization potential.
[b]Oxidation potential.
[c]Ionization potential differential.
[d]Atomic radius.
[e]Atomic number.
[f]Log AN/IPD.

and Cd. The canonical correlation between these two variates was 0.38 and accounted for 14% of the remaining variation. No other eigenvectors were significant.

Discussion

Based on the multiple regressions and canonical correlations, internal metal *CF*'s were strongly related to electrochemical properties typical of the essential elements. It appears that the oxidation potential may be a particularly good predictor of tissue incorporation. A consideration of metal chemistry in relation to the affinity of different elements for biological tissues might assist in interpreting these results.

Trace metal ions in biological tissues are bound almost exclusively by organic molecules; the most frequently occurring ligands are amino acids (Kirchgessner 1975). In biological systems metals associate with O, N, or S bearing functional groups of many metalloporphyrins, metalloenzymes, and metal-activated enzymes. The relative stabilities of Zn, Cd, Hg, and Pb complexes are dependent upon the donor ligand. As one moves to the right in a given period of the periodic table, the charge on the nucleus increases without the introduction of new valence shells, and results in a systematic decrease in atomic radii. Elements that have higher charge to radius ratios have stronger binding affinities. Ions of nontransitional elements assume a noble gas configuration and, as a result, usually react with functional groups by electrostatic attraction.

An increase in nuclear charge results in a greater force on the valence electrons and, as a result, complexes of elements such as Zn, Cd, and Hg are of a covalent nature. Cadmium and Hg have even stronger tendencies towards polar binding than Zn, and thus can substitute for Zn in thiol ligands.

The transition elements, with partly filled *d* or *f* shells, can exist in several oxidation states, an attribute that makes them particularly suitable for biological functions. These elements can fulfill many biological functions that depend upon metal reactivity. The ionization potential of many of the transition metals is high, and this is also of fundamental importance for their biochemical significance because very low ionization potentials render elements unreactive.

The size of the metal ion is important in determining metal binding preferences. Metal ions can substitute for others of similar size and this is often the basis for metal toxicity. Similarity in size is generally more important than identical charge for metal ion substitutions (Martin 1986).

The low *CF*'s for the essential elements Mn and Fe may be explained by the presence of high sediment concentrations of Mn and Fe in biologically unavailable forms, such as hydrous oxide precipitates. The tendency of these elements to precipitate relates to the fact that in 6-coordination, both have high charge to radius ratios. The greater this ratio, the more likely it is for elements to form hydroxocomplexes that precipitate in the form of polynuclear complexes (Martin 1986). In addition, Mn^{2+} and Fe^{2+} have high affinities for imidazole groups, in contrast with other divalent elements (e.g. Zn, Cu, Cd) which have higher affinities for thiol groups. Pathways for assimilation of trace essential nutrients such as Zn and Cu, then, would be more amenable to other nonessential elements that share the same affinity for thiol ligands. The binding affinities of such ligands for Fe and Mn are relatively low and Fe and Mn would not be predicted to compete effectively with Cu and Zn for protein binding sites. Thus, a combination of binding affinities and the tendency of the hydroxy ions to form insoluble precipitates may explain the low *CF*'s observed for the essential elements Fe and Mn.

Toxic metals that are widely distributed tend to be "soft Lewis acids" (e.g. Cu, Cd) that preferentially bind to "soft Lewis bases" (e.g. SH^-, S^{2-}) (Pearson 1963). Covalent bonding is associated with soft acids and bases. Toxicity is often a function of electronegativity, which is a measure of the tendency for an atom to gain, rather than lose electrons in a chemical bond. The more electronegative metals and the divalent transition metals (e.g. Cd) react rapidly with amino, imino, and sulfhydryl groups in proteins, displacing essential metals (e.g. Zn) and thereby deactivating enzymes.

As suggested by Patterson (1965), the extent to which nonessential metals are incorporated into biological tissues is likely to be a consequence of how closely their physicochemical properties resemble those of essential metals. The present study showed that concentration factors in chironomids were higher for the essential elements Zn, Cu, and Ca than for the nonessential elements Pb, Cd, and Al. There appears, as well, to be a relationship between adsorbed metal and metals in whole sediment that was explained to some degree by the properties of the elements such as atomic radius. This agrees with Jackson et al. (1980) who showed a positive relationship between ionic radius and metal release from sediment to interstitial water. The positive correlation between atomic radius and the adsorbed metal *CF* for whole sediments may also be related to the availability of the larger ions for adsorption to the larval cuticle, while the positive correlation between ionization potential and internal metal *CF* for sieved sediments may be related to the affinity of the more polar metals for protein ligands.

The positive correlation between ionization potential and concentration factors reported here reflects the importance of this property in metal metabolism, because very low ionization potentials render elements unreactive. Martin (1986) showed that some of the metal ions that form the strongest bonds undergo rapid ligand exchange, and that the exchange rates of Al^{3+}, for example, with its low ionization potential are eight orders of magnitude slower than those of Cu^{2+}. In my data, Al *CF*'s were extremely low, which was consistent with the slow ligand exchange rate that would be expected based on the low ionization potential of Al.

Conclusions

The precise combination of physicochemical properties that enhance the interaction between metal ions and biological tissues varies with the donor group of the ligands and varies among metals. Nevertheless, nonessential elements that closely resemble either Ca or Zn share those properties that promote their incorporation into biological tissues via O or N and S donor ligands, respectively.

In general, essential elements had higher *CF*'s than nonessential elements, with the exception of Fe and Mn, both of which have very high oxidation potentials, and form insoluble hydroxides. Properties of the elements that were related to the affinity of metal ions for biological tissues, such as oxidation and ionization potentials, were correlated with *CF*'s and explained 81% of the variation in *CF*'s.

Kaiser (1985) showed that parameters derived from ionization potentials and redox potentials of 15 metals correlated with metal toxicity to mice and accounted for 76% of the variability in the LC_{50} scores. From the present study, it is clear that metal accumulation by chironomids was related to metal properties,

particularly ionization and oxidation potentials, the relative importance of which varied with pH. A substantial proportion of the variability in *CF*'s was explained by physical and chemical properties of the elements, even when lakes of different pH were combined.

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Feeding Ecology of Juvenile (Age-0) Silver Hake (*Merluccius bilinearis*) on the Scotian Shelf

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Feeding patterns of juvenile silver hake (*Merluccius bilinearis*) (length range 19–90 mm) captured by midwater trawl were compared between seasons (fall and winter), years (1980 and 1981), fish lengths, and depth and time of capture. Prey selection shifted gradually with increasing fish length, from copepods at the smaller size ranges, to amphipods, euphausiids and silver hake at the larger sizes. An abrupt shift in the feeding pattern occurred as larvae metamorphosed into juveniles, but there were no similar "critical" changes during the juvenile phase itself. Cannibalism of juveniles by juveniles was pronounced and could be an important factor influencing year-class strength. Silver hake juveniles did not prey on the larvae or juveniles of other fish species, nor did they compete with them for available food, mainly because the juveniles of other species were rare during the period of greatest silver hake abundance in the pelagic zone. Evidence from abundance surveys and the feeding study suggests that increased size-at-date at the early juvenile stage, possibly due to more favourable growth and feeding conditions, resulted in increased survival. Differences in feeding patterns among fish in different size categories, and captured at different depths and times generally substantiate diel migration patterns inferred from previous vertical distribution experiments.

On a comparé les modes d'alimentation de merlus argentés juvéniles (de 19 à 90 mm de longueur) capturés au chalut flottant selon la saison (automne et hiver), l'année (1980 et 1981), la longueur des poissons, la profondeur de capture et l'époque. On a constaté que le choix des proies changeait graduellement à mesure que les poissons grandissaient, passant des copépodes, pour les poissons de plus petite taille, aux amphipodes, aux ephausiides et aux merlus argentés, pour les plus gros poissons. Le mode d'alimentation changeait radicalement lorsque les larves se métamorphosaient pour prendre la forme juvénile, mais il ne s'est produit aucun changement « critique » du même genre durant le stade juvénile comme tel. On a observé beaucoup de cannibalisme entre juvéniles : ce facteur pourrait avoir une grande influence sur l'effectif de la classe. Les merlus argentés juvéniles ne s'attaquaient ni aux larves, ni aux juvéniles d'autres espèces de poissons; ils n'étaient pas non plus en compétition avec d'autres espèces, essentiellement parce que les juvéniles des autres espèces de poissons étaient rares durant la période où le merlu argenté abondait le plus dans la zone pélagique. D'après les relevés de population et l'étude des modes d'alimentation, l'augmentation de croissance au début du stade juvénile, qui pourrait être due à une amélioration de la croissance des ressources alimentaires, a déterminé une augmentation de la survie. En général, les différences de mode d'alimentation observées selon la longueur des poissons, l'époque et la profondeur de la capture étayent les conclusions tirées au sujet des migrations circadiennes dans les expériences réalisées antérieurement sur la distribution verticale.

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Silver hake (*Merluccius bilinearis*) is considered to be one of the most important predators in the Northwest Atlantic (Bowman and Bowman 1980) and has been the focus of numerous feeding studies which have substantiated or quantified its apparent regulatory role in the ecosystem (e.g. Edwards and Bowman 1979; Vinogradov 1972, 1983; Swan and Clay 1979; Clay and Currie 1984). Only one investigation, however, has presented feeding data on age-0 fish, and this was restricted to material collected by bottom trawls (Bowman 1981). Adequate information on the feeding of pelagic juvenile silver hake is required for a complete assessment of its importance in the food web. On the Scotian Shelf, age-0 silver hake dominate the juvenile fish population in the pelagic zone during fall and may compete with or prey upon the early life history stages of other commercially important species.

Recent discussion on the causes of variable recruitment in rcially important fisheries has considered factors associated with larval survival, such as the spatial and temporal "match–mismatch" of larvae and their food (Cushing 1972) and "larval retention" within prevailing but variable oceanographic entities (Iles and Sinclair 1982). Little attention has been devoted to the juvenile stage. In addition to elucidating inter-specific effects such as competition among juveniles, our study of juvenile silver hake feeding ecology promised to provide insight into the factors governing recruitment to the important commercial fishery for the species (1989 Total Allowable Catch on

the Scotian Shelf is 235 000 metric tons). Silver hake yearclass strength, as measured by annual juvenile midwater trawl surveys, is highly variable (Koeller et al. 1986) and may be related to differences in the availability of suitable food organisms at critical periods during the juvenile stage between years.

The cooperative Canada–USSR age-0 silver hake abundance surveys, begun in 1978, afforded an opportunity to collect material on fish feeding patterns from a wide area during the period of their greatest abundance in the pelagic zone. In addition, diel vertical migration and comparative fishing studies designed to improve survey methods provided material for describing changes in feeding with time and depth. Since migration patterns inferred from trawl catch data are often ambiguous, the material was also examined with the intention of substantiating previous vertical migration experiments.

Methods and Materials

Samples of pelagic juveniles were obtained in October 1980 and 1981 during the annual abundance surveys conducted on the Scotian Shelf by Canada and the USSR, and during an independent Canadian survey conducted in January 1981. In addition to fishing at randomized locations for abundance estimates, vertical distribution experiments and comparative fishing were conducted which sampled juveniles at different depths and times of day at the same site (Fig. 1). All fish examined for gut contents were obtained using the Soviet 13.6-m "fry" trawl or the International Young Gadoid Pelagic Trawl (IYGPT) fished either near bottom, throughout the water column in three steps (near bottom, midwater, and near surface) or within predefined depth strata as described in Koeller et al. (1986). Fish were preserved whole in buffered 5% formalin. A total of 845 specimens were subsampled randomly by 2-mm length strata from the preserved material to obtain fish spanning the maximum size range (19–90 mm overall) for each sampling area, time period, or depth strata.

Silver hake lengths were determined using a dissecting microscope equipped with an ocular micrometer (standard length ± 1.0 mm). Fish lengths were not adjusted for shrinkage due to preservation. Stomach and intestines were removed for enumeration and measurement of prey. Items recovered from the mouth and esophagus were discounted as possible instances of net feeding or regurgitation. Unless otherwise indicated, analyses were based on nonempty stomachs, thus eliminating fish which had not been feeding, or had regurgitated gut contents during capture or preservation. Subsampling was not required as prey items generally numbered <100 per fish.

All prey items were identified to species and developmental stage if possible and measured (± 0.1 mm) for total length (amphipods, euphausiids, decapods and mysids), metasomal length (copepods), or standard length (fish larvae). Wet weight values for prey items were estimated using length–weight relationships available from the literature or derived during the study. A list of prey items and abbreviations used in the figures is given in Table 1.

Results

Changes in Prey Composition with Fish Length

In October 1980, age-0 silver hake were relatively small (range 19–57 mm) and the smallest were undergoing metamorphosis from the larval stage (Fig. 2). This occurs at approximately 20 mm (Fahay 1983). Calanoids were the dominant food items in guts of fish up to about 40 mm in length. Fish >40 mm shifted feeding preferences slightly to include larger noncopepod items such as amphipods, mysids, and euphausiids, but calanoids continued as important food items

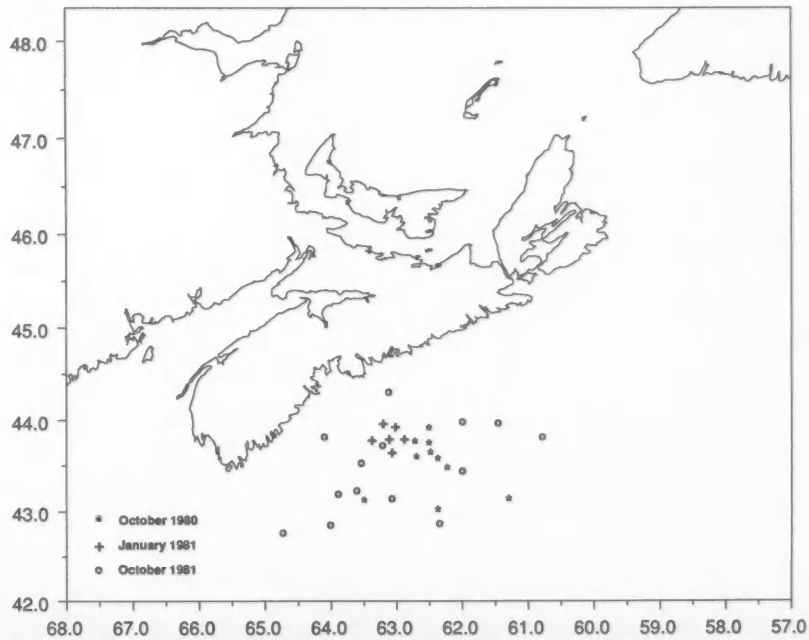

FIG. 1. Location of sampling stations on the Scotian Shelf where juvenile silver hake were collected for gut analyses.

TABLE 1. List of prey items found in juvenile silver hake guts and abbreviations used in the figures. Scotian Shelf 1980 and 1981.

Copepods	
Paracalanus parvus copepodite stage V, males and females	*P.*par.5-*M-F*
Centropages typicus copepodite stages III and IV, V, males, and females	*C.* typ.3-4 *C.* typ.5 *C.* typ.*M* *C.* typ.*F*
Clausocalanus spp. stage V, males and females	Claus. 5-M-F
Parastephos sp., males and females	Parast.M Parast.F
Temora longicornis copepodite stage V and females	T.long.5-F
Metridia lucens copepodite stages IV and V, males, and females	M. luc.4-5 M. luc.M M. luc.F
Aetidius armatus copepodite stages V, males and females	A. arm.5-M-F
Calanus finmarchicus copepodite stages IV and V, males, and females	Cal.fin.4-5 Cal.fin.M-F
Calanus hyperboreus copepodite stage V	Cal.hyper.5
Candacia armata copepodite stages IV and V, males, and females	Can.arm.4-5 Can.arm.M Can.arm.F
Amphipods	
Parathemisto gaudichaudii	Parath.gau.
Other amphipods	Other amphipods
Euphausiids and Mysids	
Meganictyphanes norvegica	Mega.nor.
Neomysis americanus	Neomysis
Euphausiids and mysids (other than *M. norvegica* and *N. americanus*)	Euph./mysid
Decapods	
Dichelopandalus leptoceras	Di-chelopan
Other decapods	Other decapods
Other prey	
Merluccius bilinearis	Silver hake
Other nonfish prey, including Pteropoda, Larvacea, Thaliacea, and Chaetognatha	Others

even for the largest fish. Cannibalism was evident in fish as small as 22–25 mm, but it increased significantly after 46 mm to over 25% of gut contents by weight. Fish larvae or juveniles other than silver hake were conspicuously absent from the gut contents. Fish collected in January 1981 ranged from 31 to 90 mm, indicating substantial growth in the intervening winter months. Feeding patterns were similar to October 1980 for fish in the same size ranges (31–43 mm), but the copepod diet was distinctly less diverse than in October. Euphausiids emerged as the most important food item in fish >46 mm. Cannibalism was evident only in fish >76 mm. Fish in October 1981 were larger than in October 1980, with a range (33–90 mm) similar to that seen in January 1981 for the previous year class. Diet composition and changes in feeding with size category were similar to October 1980, with an important exception: the copepod diet in October 1981 was more diverse than in October 1980. Fish in the largest size category (76–90 mm) showed a marked increase in cannibalism, as in January. Cannibalism by smaller fish (<57 mm) was significantly lower than during the previous October.

Changes in Prey Size with Fish Length

Although mean prey size generally increased with fish length (Fig. 3) there were also consistent differences in mean prey size between the three sampling times, even within overlapping size ranges (37–57 mm) and at the same time of year (October 1980–81). Mean prey size was similar in October 1980 and January 1981 for 31–43 mm fish, but in larger fish mean prey size was consistently larger in January than either of the October samplings due to the dominance of euphausiids in January versus copepods and amphipods in October. The large mean prey size in the largest size category in October 1981 was due to the high degree of cannibalism in this group.

The smallest larvae were restricted to feeding on small prey (copepod nauplii) of similar size, as indicated by the narrow error bars in Fig. 4. Between 6–16 mm in length larger fish ate progressively larger prey of a greater size range. Between 16–25 mm, larvae or juveniles became more selective and fed mainly on larger copepods. Subsequently, average prey size again increased with predator length and the size range of prey taken increased dramatically (Fig. 4).

Feeding versus Depth

Changes in feeding with depth (Fig. 5) can be interpreted in light of available information on the vertical distribution of prey species. In October 1980 *Metridia lucens* and *Candacia armata* increased in importance as food items for fish caught in shallower depth zones. Both species have been reported at depths less than 50 m at night (Sameoto 1984), the time when most of our trawl sets were conducted. *Centropages typicus* inhabits surface layers at all times. Its presence in guts of silver hake from the deeper sets indicated capture of some fish near the surface by the nonclosing trawl gear and/or movement of fish between depth layers. The presence of sand particles (not shown) and the bottom-living copepod *Parastephos* sp. in guts of fish captured well above bottom in October indicated movement of predators between depth layers. In January 1981, *M. lucens* and *Parathemista gaudichaudii* increased in importance with decreasing depth of capture. Both organisms generally concentrate in the upper 50 m at night. Similarly, in October 1980, benthic amphipods (*Rachotropis* sp. and *Byblis gaimardi*), decapods (*Dichelopandalus leptoceras*) and sand were present in greater proportions in fish caught in the deeper strata. Note that depth stratification by fish size should not have influenced these results because juveniles of all sizes occupy all depth levels during the night feeding period (Koeller 1981).

Feeding versus Time

Koeller et al. (1986) concluded that the low catchability of age-0 silver hake during daylight hours was due to a near bottom distribution by day. Feeding patterns in October 1981 (Fig. 6) showed a decrease in the diversity of organisms in guts between early morning and early evening, as would be expected if fish were feeding in a restricted part of the water column (i.e. near bottom) during daylight hours. There were no discernible patterns in the October 1980 and January 1981 data.

Predator Abundance and Size

Silver hake were the most abundant juvenile fish present on the Scotian Shelf in all years during the fall survey period (Table 2). With few exceptions, juveniles of other commercial species such as witch flounder (*Glyptocephalus cynoglossus*), yellow-

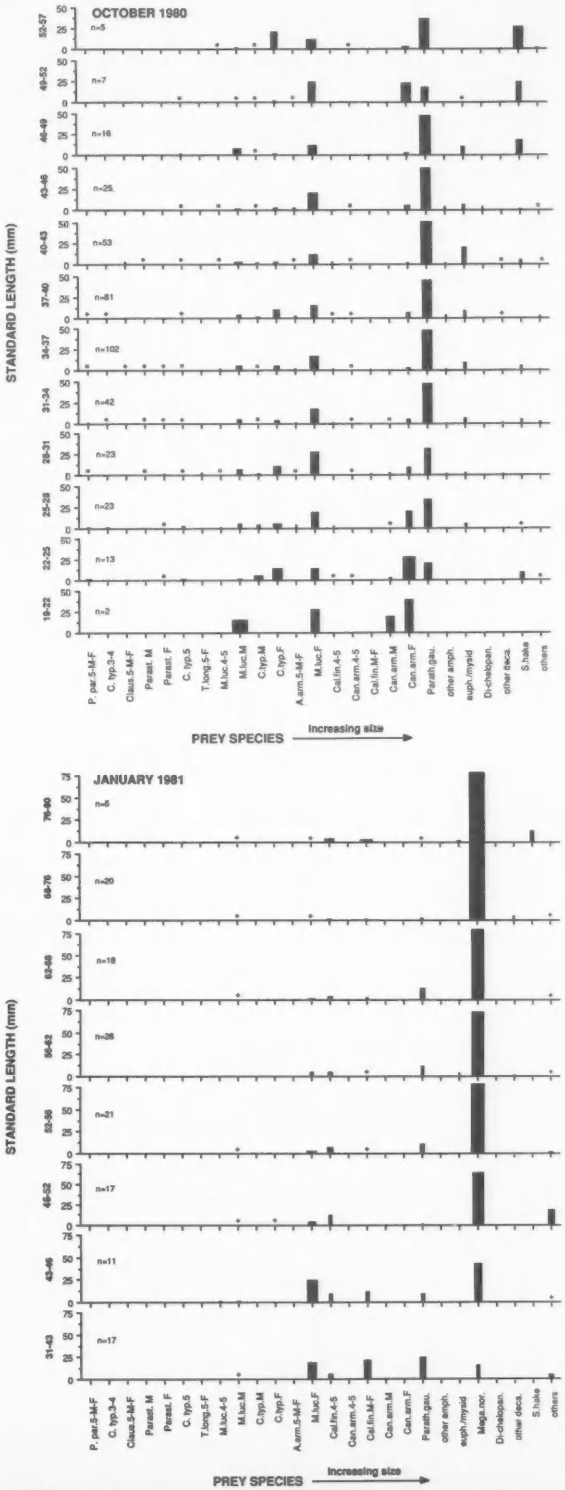

FIG. 2. Feeding patterns of juvenile silver hake by size group, expressed as the percentage of the total gut contents weight (bar height)

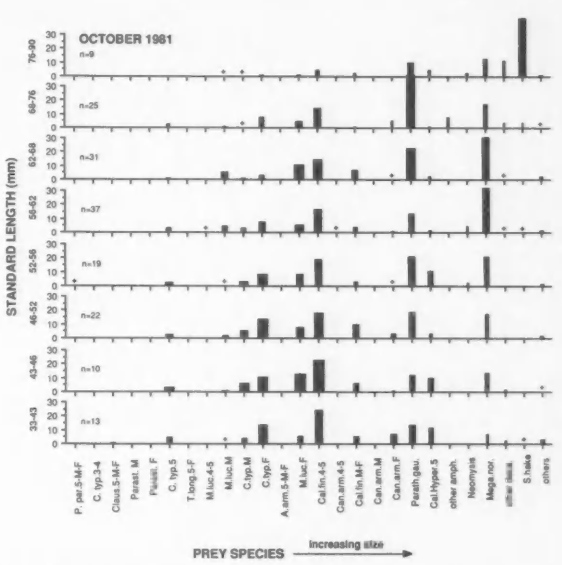

FIG. 2. (*continued*)
and frequency of occurrence of prey in the gut (bar width) in October 1980, January 1981, and October 1981. "+" represents present, but too rare to show on graph.

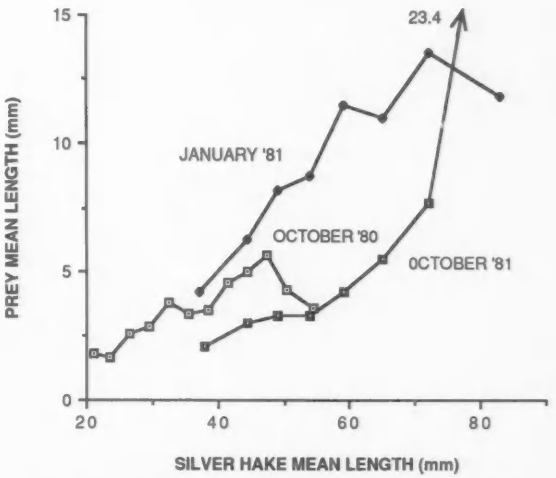

FIG. 3. Relationship between mean prey length and juvenile silver hake length in October 1980, January 1981, and October 1981.

tail flounder (*Limanda ferruginea*), squid (*Illex illecebrosus*), American plaice (*Hippoglossoides platessoides*), haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes* sp.), cod (*Gadus morhua*), and herring (*Clupea harengus*) were several orders of magnitude less abundant.

Figure 7 shows the relationship between the juvenile silver hake abundance index and mean fish length during each year of the Canada–USSR survey. The two years in which feeding data were collected represented the years of largest mean fish size and greatest abundance (1981) and the smallest mean size and second lowest abundance (1980).

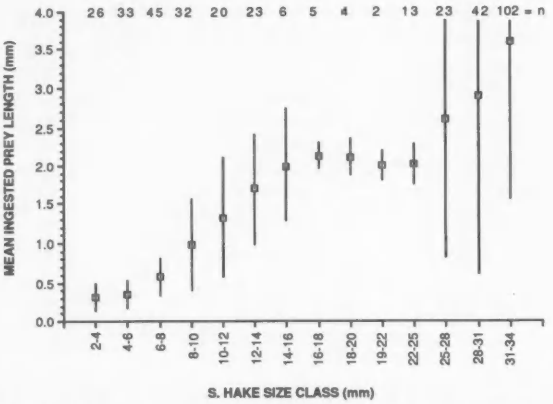

FIG. 4. Relationship between mean prey length (± 1SD) and silver hake length including early larval to juvenile silver hake. Data for larval and early juvenile stages (2–20 mm) from August 1978 (Coates-Markle 1982), and for larger juveniles (19–34 mm) from October 1980, this study.

Discussion

Results from this study generally substantiate diel and ontogenetic migratory behaviour of juvenile silver hake larvae and juveniles previously inferred from trawl catch data. Larvae are found near the surface (Fahay 1973; Sameoto 1984) where they feed on smaller planktonic organisms such as copepod larvae and younger copepodites (Coates-Markle 1982). During metamorphosis at about 20 mm the size range of prey items narrows and mean prey size remains constant while fish length increases, possibly due to decreased swimming abilities associated with physiological changes during metamorphosis (Fig. 4). Koeller et al. (1986) concluded that shortly after metamorphosis silver hake begin a strong diel vertical migration during which they are near or on the bottom by day and throughout the water column at night, a behaviour also observed by Bowman and Bowman (1980) in adult silver hake. The wide size range and type of prey items taken, including surface and bottom-living copepods, confirms that juveniles feed over a wide depth range at night (Fig. 5). During daylight both the number and size of juveniles available to pelagic trawls decreases greatly, presumably due to a near- or on-bottom distribution (Koeller et al. 1986). The importance of benthic organisms does not increase during daytime as would be expected by an on-bottom distribution, but a decrease in gut content diversity (Fig. 6) does suggest that the fish are feeding in a restricted depth range (i.e. near bottom). Daytime feeding data may not be completely representative due to the small number of fish available for study during this period.

Previous studies have shown that silver hake 10–40 cm in length feed mainly on euphausiids, and that larger fish are piscivorous (Vinogradov 1972, 1983; Swan and Clay 1979; Clay and Currie 1984). This change occurs gradually over the pre-

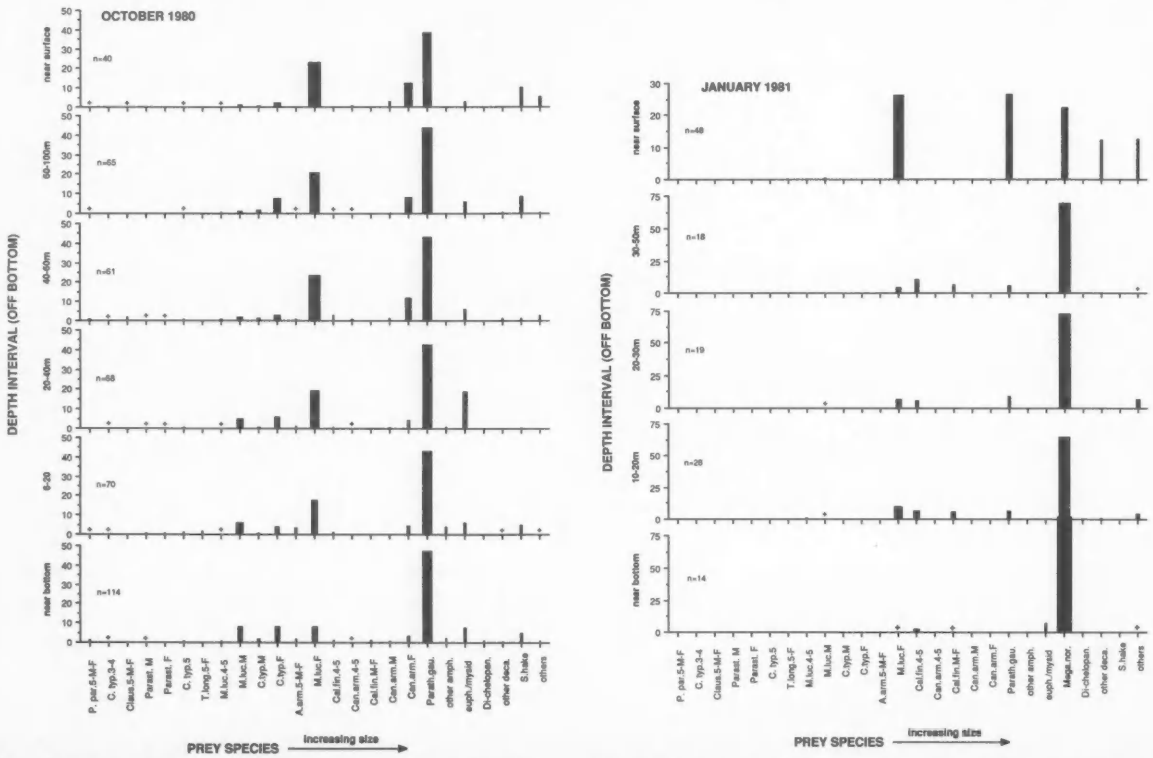

FIG. 5. Feeding patterns of juvenile silver hake at different depths expressed as the percentage of the total gut contents weight (bar height) and frequency of occurrence of prey in the gut (bar width) in October 1980 and January 1981. "+" represents present, but too rare to show on graph.

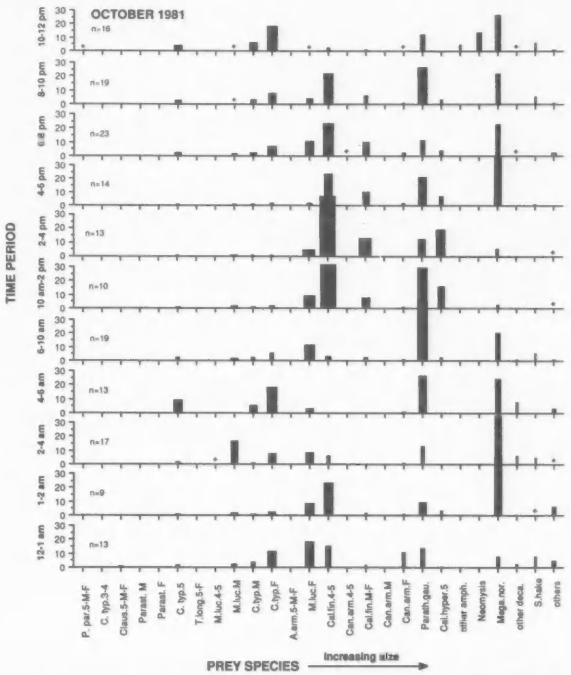

FIG. 6. Changes in feeding patterns of juvenile silver hake with time of day expressed as the percentage of total gut contents weight (bar height) and frequency of occurrence of prey in the gut (bar width) in October 1981. "+" represents present, but too rare to show on graph.

dator length range. The present study shows that the change from copepods to euphausiids as prey items in smaller silver hake is also a gradual one which is still not completed when silver hake are 90 mm long (Fig. 2). There is no rapid shift in the diet of juveniles that can be associated with ontogenetic vertical migration or other critical life history change such as occurs in haddock (Koeller et al 1986; Mahon and Neilson 1987), but such a change does occur at the larval–juvenile transition (Fig. 4). Silver hake can be highly selective while feeding at certain depths and times, as indicated by the presence of a rare and new species of bottom-living copepod *Parastephos* (T.E. Bowman, Smithsonian Institute, pers. comm.) However, the relatively large differences in dominant prey species and in the predator/prey size relationship in fish of similar size between sampling times (Fig. 3) indicates that silver hake juveniles are opportunistic, adapting to the available zooplankton population.

Both Vinogradov (1983) and Clay and Currie (1984) emphasize the importance of cannibalism in older silver hake, to the extent that it is considered an important factor limiting production. The present study shows that significant cannibalism can already occur at the early juvenile stage, at times exceeding 40% by weight of the gut contents. In 1981, when the juvenile silver hake abundance index was the highest in the 9-yr Canadian–USSR survey series, silver hake was an important food item only for the largest size category (76–90 mm), but was virtually absent from the guts of smaller (<57 mm) fish. In 1980, when abundance was the second lowest and mean fish length was the third lowest recorded, silver hake were more significant components of the diet (up to 25% by weight) of smaller fish, suggesting that cannibalism increased during unfavourable years (Fig. 2). While it is apparent that cannibalism can be an important factor in establishing silver hake yearclass size, the complete absence of other species as prey shows that at this life history stage, silver hake predation does not influence survival of other commercially important fish species.

On the Scotian Shelf, silver hake spawn during July–October, a time period substantially different from other commercially important species (O'Boyle et al. 1984). Silver hake minimize competition with other species by occupying the pelagic zone as age-0 juveniles at a time when juveniles of other species are rare (Table 2). But do juvenile silver hake compete among

TABLE 2. Abundance indices (stratified mean catch/tow) of juvenile fish (defined as <100 mm in length) obtained from the cooperative Canada–USSR juvenile silver hake surveys. The myctophid category, due to small size, includes both adults and juveniles.

Species	Year								
	1978	1979	1980	1981	1982	1983	1984	1985	1986
Merluccius bilinearis	168.15	172.67	27.00	643.26	7.32	227.39	42.86	275.10	233.01
Myctophidae	2.19	3.24	10.89	1.58	30.15	2.91	14.34	2.99	3.66
Maurolicus muelleri			0.01				8.86	0.54	0.61
Glyptocephalus cynoglossus	3.65	2.16	3.32	1.90		0.42	0.01	0.57	0.23
Urphysis chuss	0.26	2.60	0.55	2.86	0.10	0.30	0.07	0.34	0.30
Illex illecebrosus	0.26	0.13	0.16	3.65	0.28	0.03	0.85	0.48	0.09
Hippoglossoides platessoides		1.67	1.54	0.18	0.60	0.44	0.11	0.07	0.05
Prionotus evolans				4.31					
Argentina silus	0.06	4.05	0.70	0.27	0.02	0.14		0.10	
Melanogrammus aeglefinus	0.07	1.35	1.42	0.14	0.13		0.03	0.01	
Peprilus triacanthus	0.07	0.05	0.94	0.34		0.02		0.74	
Ophichthus puncticeps						3.08			
Sebastes sp.	0.09	0.15	0.24	1.16	0.15	0.39	0.01	0.71	0.55
Gadus morhua	0.98	0.13	0.36	0.05	0.48	0.16	0.01	0.01	
Lophius americanus	0.76	0.09	0.18	0.49	0.02	0.08		0.10	0.07
Scomberesox saurus	0.98		0.22						
Clupea harengus	1.11	0.38							0.01
Limanda ferruginea	0.35	0.38	0.24						
Sternoptychidae			0.49	0.01	0.12			0.11	0.50
Citharichthys arctifrons		0.04	0.17	0.18					

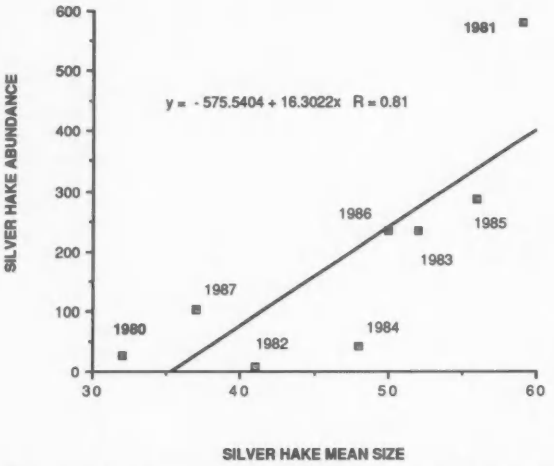

FIG. 7. Relationship between the juvenile silver hake abundance index obtained from the Canada–USSR cooperative surveys and mean fish length. The linear regression coefficient is significant at $p<0.05$. The first two years (1978, 1979) of abundance estimates are excluded due to different survey methods used during these years. Note the extreme values of the two study years (1980, 1981).

themselves – or more generally, does food availability limit growth and survival? The positive correlation between the juvenile abundance index and fish length (Fig. 7) indicates that larger size (possibly reflecting increased growth) results in greater survival. The larger size of fish in October 1981 may have resulted from more favourable feeding conditions that can be inferred from the greater diversity of the copepod diet at that time (Fig. 2). These observations support the hypothesis that biological factors such as food and growth are more important to survival during the early juvenile stage than during the larval stage, when the influence of physical oceanographic factors may prevail. This hypothesis could be useful in approaching the complex problem of determining how a year class is established in commercially important marine fish species.

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Stable Isotope Analysis of Carbon Flow in a Tundra River System

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Stable isotope analysis was used to identify the major sources of carbon utilized by fish and aquatic invertebrates in the Koroc River, a tundra river system in northern Quebec. Juvenile arctic char (*Salvelinus alpinus*), together with adults and juveniles of other species of fish in freshwater, obtained their carbon from either allochthonous or autochthonous sources within the river system, via the invertebrate fauna. However, adult anadromous char caught in the river clearly derived their biomass carbon from feeding at sea. Despite the limited development of riparian vegetation throughout much of the lower river catchment, terrestrial organic matter was the most likely source of energy fueling the animal communities of small tributary streams and rapids of the mainstem Koroc. In contrast, epilithic algae made a significant contribution to food chains within Alik Lake, a deep basin along the main river channel. Aquatic mosses appeared to be of, at most, tertiary importance as a source of energy to the animal communities of the lake, despite their considerable biomass.

On s'est servi de la technique d'analyse des isotopes stables pour identifier les sources majeures de carbone utilisées par les poissons et les invertébrés aquatiques dans la rivière Koroc, système fluvial situé dans la toundra au Nouveau-Québec. Les jeunes ombles chevaliers (*Salvelinus alpinus*), ainsi que les adultes et les jeunes d'autres espèces de poissons vivant en eaux douces, ont obtenu leur carbone de sources soit autochtones ou allochtones à l'intérieur du réseau hydrographique, via la faune des invertébrés. Cependant, les ombles anadromes adultes capturés dans la rivière tiraient manifestement le carbone de leur biomasse de leur alimentation en mer. En dépit de la croissance limitée de la végétation riveraine dans la majeure partie du bassin inférieur de la rivière, c'est la matière organique d'origine terrestre qui constituait très probablement la source d'énergie qui alimentait les communautés animales des petits tributaires et des rapides du bras principal de la rivière Koroc. Par contre, les algues épilithiques contribuaient de façon significative aux chaînes alimentaires à l'intérieur du lac Alik, bassin profond qui longe le lit principal de la rivière. Les mousses aquatiques ont semblé venir, tout au plus, au troisième rang comme source d'énergie des communautés animales du lac, malgré leur biomasse considérable.

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Knowledge of the pattern of energy flow and material cycling is essential to our understanding of how ecosystems function. Early stream ecologists recognized the importance of allochthonous carbon as a major source of energy fueling forest stream ecosystems (see Hynes 1975). Subsequent research, particularly in the temperate forest systems of North America, has led to the development of a generalized model of stream structure and function, which emphasizes the sources of energy and nutrients and the way in which these materials move through stream ecosystems (Vannote et al. 1980; Newbold et al. 1982; Minshall et al. 1983, 1985). As a consequence, most of our knowledge of the structural and functional organization of lotic systems is derived from studies of streams in temperate regions.

Autochthonous sources of carbon, however, may make a significant contribution to the energy pathway of some lotic systems (Minshall 1978), such as desert streams and others that do not flow through dense forest (Busch and Fisher 1981; Naiman 1981; Rounick et al. 1982; Winterbourn et al. 1986). In contrast, tundra river systems appear to be similar in function to many temperate streams in that they are dependent on allochthonous sources of carbon, despite a conspicuous lack of riparian vegetation (Peterson et al. 1985a, 1986). Very little is known about the flow of energy in tundra streams but such information is essential to the successful management of arctic fisheries and the prediction of how such systems will respond to human disturbance.

Many river systems entering Ungava Bay, northern Quebec, support populations of the anadromous arctic char (*Salvelinus alpinus* L.), which may account for as much as half of the annual food supply in some traditional Inuit communities (Balikci 1980). In addition to this subsistence harvest, sport fishing for arctic char is an important source of income for many Inuit, and commercial fishing is coming to be regarded as a potentially significant source of revenue (Power and Barton 1987). While the general biology of arctic char is fairly well documented (Moore 1975a, b; Gillis et al. 1982; Johnson and Burns 1984; Dempson and Green 1985), little is known about the relationship between this species and other components of its riverine habitat, particularly with respect to energy flow.

The aim of this study was to determine the principal source, or sources, of energy fueling the invertebrate and fish communities of a tundra river system, using stable carbon isotope

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tracing. This technique provides a powerful alternative approach to the traditional methods of assessing food resources used by consumers (see Fry and Sherr 1984; Rounick and Winterbourn 1986; Peterson and Fry 1987 for reviews). Stable isotope ratios of consumer tissue have been used to identify the major carbon pathways in many systems, including rivers and lakes (e.g. Rau 1980; Rounick et al. 1982), estuaries and salt marshes (e.g. Peterson et al. 1985b; Jackson et al. 1986), and the sea (e.g. McConnaughey and McRoy 1979; Fry et al. 1982). We used this technique to describe the major carbon pathways within the river system and, in particular, to assess the importance of riverine food chains to arctic char.

Study Area

Sampling sites were located within the lower catchment of the Koroc River, a fourth-order river which discharges into Ungava Bay approximately 30 km north of Kangiqsualujjuaq, northern Quebec (Fig. 1). The Koroc originates in the Torngat Mountains on the Quebec/Labrador border and has a total drainage area of about 4050 km^2. The river bed consists of granitic boulders and bedrock ledges in tributary streams and mainstem rapids, while sand and fine gravel are the predominant substrata in the main channel from Hulik Lake to above Alipaaq Creek. Winter ice cover typically breaks up in mid-June and discharge increases erratically depending on weather through mid-July as snow melts in the Torngats, then generally declines until freeze-up in late October. River water is characterized by low conductivity (10–30 $\mu S \cdot cm^{-1}$) and is usually very clear with underwater visibility noted by divers at greater than 8 m, except during a brief period of maximum snowmelt when visibility was limited to 0.5–2 m (Stenzel 1987). During August 1987, three water samples, filtered through Whatman GF/C filters, contained 456 ± 11 $\mu g \cdot L^{-1}$ of suspended material ($\bar{x} \pm 1$ SE).

Despite its relatively low latitude (58°46′N), the climate of the Koroc basin is subarctic and the northern tree-line parallels the coast of Ungava Bay coincident with the mouth of the river. Sparse to moderately dense stands of black spruce, willow, and birch occur in sheltered valleys along the Koroc but rarely more than 40 m above river level. The dominant type of vegetation throughout most of the basin is tundra, consisting of lichens, mosses, and dwarf shrubs. A list of common species found in the study area is given below.

Samples of fish, invertebrates, and plant material for stable isotope analysis were collected from nine sites within the lower part of the river system (Fig. 1). Sites 1 and 2 were located in the Koroc estuary, near the mouth of the river. The main river channel was sampled along the margin of the first set of rapids (Site 3) where the river empties into the estuary, and at a second set of rapids (Site 4) at the upper end of Alik Lake. Alik Lake, a deep basin of the main river channel (maximum depth approximately 75 m), was sampled along the shore at depths less than 1 m (Site 5) and at a depth of 10 m in the centre above the first rapids (Site 6). Dredging in deeper water (40 m) did not yield enough animals for isotopic analysis. Three small tributary streams were also sampled, all of which drain small lakes: Aapiq Creek enters the upper end of Alik Lake (Site 7), Onatualluq Creek enters the river above Hulik Lake (Site 8), and Alipaaq Creek (Site 9) enters the river about 30 km above the estuary (Fig. 1). Several other sites were also visited, but insufficient material was obtained for isotope analysis.

Materials and Methods

All collections were made between the 7th and 20th August 1987. A small seine net or hand net was used to catch juvenile fish at night with the aid of a gasoline lantern, along the shore of Alik Lake and from the mouths of Alipaaq and Aapiq Creeks. Sticklebacks (*Gasterosteous aculeatus*) and sculpins (*Myoxocephalus* sp.) were caught in Alik Lake and the estuary, respectively, using a simple dredge with a rectangular opening 30×50 cm and a tapered collecting net of 1-mm mesh. Adult arctic char, brook trout (*Salvelinus fontinalis*), and lake trout (*Salvelinus namaycush*) were caught in the mainstem Koroc and Alik Lake by angling. Muscle tissue from five additional arctic char was provided by T. Boivin: all were sexually immature, ranging from 43.5 to 52.5 cm fork length, weighing 875 to 1700 g, and were caught in gill-nets from Hulik Lake during November 1985.

Benthic invertebrates were collected from Sites 3–5 and 7–9 using a D-frame net (240-μm mesh). Large rocks were turned and scrubbed to remove attached plants and animals, and areas of gravel or sand were vigorously disturbed by kicking with the net held downstream. Aquatic mosses and accumulations of coarse detritus were also collected and sorted for invertebrates. Plankton was collected from Alik Lake (Site 6) and the estuary (Sites 1 and 2) by horizontal tows of a 0.5-m diameter conical net (156-μm mesh) at depths of 1–3 m. The epibenthos at these deeper sites in Alik Lake and the estuary was sampled with the dredge.

Samples of aquatic plants and coarse detritus were removed from fish and invertebrate collections, supplemented with material gathered by hand, and rinsed thoroughly to remove animals and fine detritus. Small areas (5 cm^2) of the surfaces of rocks in the littoral margins of Alik Lake were scraped to provide an estimate of the standing crop of epilithic periphyton and material for isotope analysis. Samples of the major terrestrial plants were collected around Alik Lake and Alipaaq Creek. The tundra groundcover in parts of the valley had been reduced to a thick mat of loose peat through trampling by caribou. Samples of this material also were collected as it was considered to be a likely source of organic matter entering the river during periods of heavy rainfall or snowmelt.

Invertebrates were sorted live from the bulk samples and vouchers of each taxon preserved in 70% ethanol. Vouchers of terrestrial plants were pressed and dried. A small piece of muscle tissue was removed from each of the larger fish, while small sculpins, sticklebacks and large invertebrates were eviscerated. Smaller invertebrates were kept alive in fine mesh cages until their guts had emptied. All samples of animal and plant tissue were oven dried at 50–100°C, wrapped in aluminum foil and sealed in plastic bags with desiccant.

Stable Isotope Analysis

Subsamples of approximately 10 mg dry weight of fish, invertebrate and plant matter were pulverized into a fine powder. Crustaceans and molluscs were first acidified with 1 N HCL, washed with distilled water and redried to prevent contamination of the organic carbon from the carbonate fraction in shell or exoskeleton (Haines and Montague 1979). Several individuals of some of the smaller taxa were pooled to obtain an adequate sample. All of the organic carbon present in these samples was then oxidized in a Leco furnace (Drimmie 1976) and the resulting CO_2 purified and analysed in a Micromass

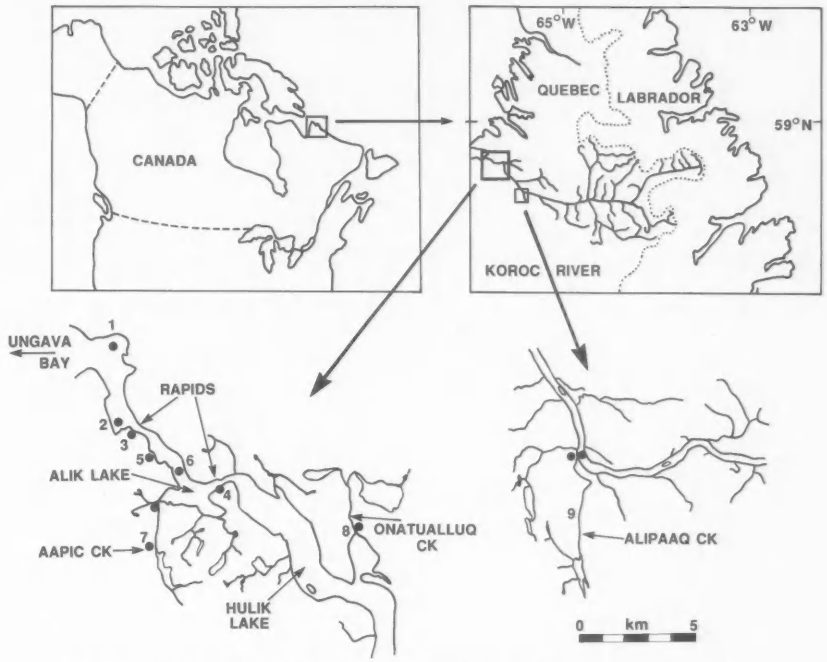

FIG. 1. Location of the Koroc River system and the nine sites sampled in this study.

903 triple collector ratio mass spectrometer (Vacuum Gage Co.). Ratios of ^{13}C to ^{12}C were expressed as $\delta^{13}C$ (‰), where

$$\delta^{13}C = \frac{^{13}C/^{12}C \text{ sample} - {}^{13}C/^{12}C \text{ PDB standard}}{^{13}C/^{12}C \text{ PDB standard}} \times 1000.$$

The PDB standard refers to the international carbonate standard prepared from the fossil skeleton of a belemnite from the PeeDee formation, South Carolina (Craig 1957). The analytical precision, based on six measurements of a graphite standard over a 9-wk period, was 0.5% ($\bar{x} = -25.99$; 1 SE = 0.12‰). In addition, eight pairs of replicate samples of fish tissue were found to have a mean difference (±1SE) of 0.27 ± 0.08‰.

Results

Terrestrial and Aquatic Vegetation

The most common riparian species in the lower catchment of the Koroc River were willow (*Salix planifolia*), alder (*Alnus crispa*), and birch (*Betula glandulosa*). These grew to heights of up to 2.5 m along some stream margins but quickly decreased in size with increasing altitude on wet hillsides. Tamarack (*Larix laricina*) and black spruce (*Picea mariana*) were also common on the valley slopes, though few individuals were more than 4 m in height. The mean $\delta^{13}C$ value of leaves from these five species was −27.8‰, the same as that found for decomposing leaves collected from the shallows of Alik Lake and small tributary streams (Fig. 2). On an areal basis, the ground cover consisted primarily of lichens (*Cladina stellaris, Arctoparmelia centrifuga, Haemotomma lapponicum*), mosses, and other low-growing plants such as *Empetrum nigrum, Ledum decumbens*, and in wetter areas, *Carex saxatilis*. These species,

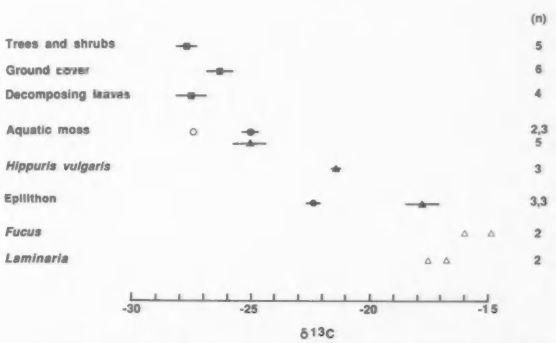

FIG. 2. Stable carbon isotope ratios ($\delta^{13}C$) of terrestrial (■) and aquatic (○ = mainstem rapids; ● = small tributary streams; ▲ = Alik Lake; Δ = estuary) plant material from the Koroc River system and its catchment (mean ± 1SE; n = number of samples).

together with the samples of loose detritus, were slightly more ^{13}C enriched with a mean $\delta^{13}C$ of −26.4‰ (Fig. 2).

Aquatic plants showed considerable variation in $\delta^{13}C$ values and were more ^{13}C enriched than most terrestrial plants. Aquatic mosses in the tributary streams and mainstem rapids were found growing only in small clumps on stones, but formed a thick carpet over much of the bottom of Alik Lake at depths of 3–10 m. Samples from the tributary streams and Alik Lake had similar mean $\delta^{13}C$ values (−25.1‰), however, small clumps from the rapids were more ^{13}C depleted (Fig. 2). The only other aquatic macrophyte recorded, *Hippuris vulgaris*, was found in small patches growing up through the moss in Alik Lake at depths of 3–5 m. This species was far more ^{13}C enriched than the mosses, with a mean $\delta^{13}C$ value of −21.5‰ (Fig. 2).

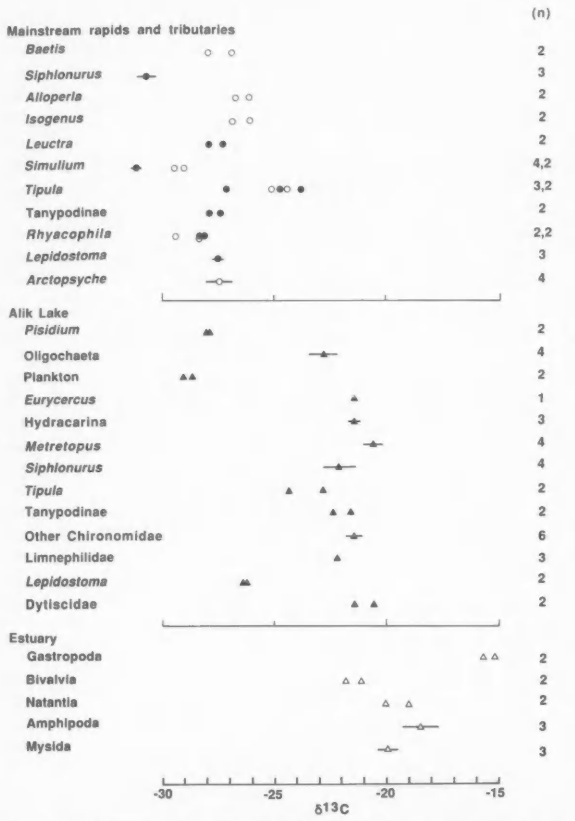

FIG. 3. Stable carbon isotope ratios ($\delta^{13}C$) of aquatic invertebrates from the Koroc River system (mean ± 1SE; n = number of samples. Symbols as for Fig. 2.)

Despite the lack of shading by terrestrial vegetation, stones forming the beds of tributary streams and at depths of less than 1 m in the mainstem rapids appeared to be free of epilithic algae. As a consequence, we were unable to collect sufficient material for stable isotope analysis. Rock scrapes from a depth of about 35 cm along the margin of Alik Lake, however, yielded a mean (±1SE) dry weight of 1.2 ± 0.1 mg·cm^{-2}. This epilithon was the most ^{13}C enriched of the samples from freshwater with a mean $\delta^{13}C$ value of -17.8‰ (Fig. 2). The only other epilithon sampled was a thick, brown mat on stones at the outlet of the headwater lake above Aapic Creek. This consisted mainly of fungus, decomposing moss fragments and diatoms, and had a mean $\delta^{13}C$ value of -22.4‰.

The dominant marine macroalgae were *Fucus*, found in the lower intertidal and shallow subtidal zones of the estuary, and *Laminaria*, which was abundant at depths of about 4–5 m below low tide. The $\delta^{13}C$ values of samples of kelp were similar to that of epilithic algae from Alik Lake but *Fucus* was slightly more ^{13}C enriched (Fig. 2).

Aquatic Invertebrates

The mean $\delta^{13}C$ values of the more common aquatic invertebrates from the small tributary streams and rapids of the main river channel were similar to that of leaves of the terrestrial vegetation (Fig. 3). Notable exceptions were larvae of *Simulium* spp. and nymphs of *Siphlonurus quebecensis*, collected at the outfall of the headwater lake on Aapic Creek. Both of these taxa were ^{13}C depleted with respect to other lotic invertebrates and had mean $\delta^{13}C$ values of only -31.0 and -30.5‰, respectively. Blackfly larvae and *Rhyacophila* from the mainstem rapids were also ^{13}C depleted with respect to the rest of the lotic fauna, but to a lesser extent. Larvae of *Tipula* were found in the finer sediments of the tributary streams and mainstem rapids, and generally were more ^{13}C enriched than other taxa (Fig. 3). These larvae showed considerable variation in $\delta^{13}C$ values between the tributary streams, ranging from -27.0‰ in Alipaaq Creek to -23.7‰ in Onatualluq Creek.

In general, invertebrates from Alik Lake were more ^{13}C enriched than those in the tributary streams and rapids of the main river channel (Fig. 3). Of the taxa found in both lotic and lentic habitats, *Siphlonurus quebecensis* and Tanypodiinae showed a marked difference in $\delta^{13}C$ values. Samples of the former species from Alik Lake were ^{13}C enriched by 10‰ more than those from Aapic Creek. In contrast, $\delta^{13}C$ values of *Lepidostoma prominens* showed little habitat difference, indicating a similar ultimate dietary source. Likewise, $\delta^{13}C$ values of lentic samples of *Tipula* were similar to those for Onatualluq Creek and the mainstem rapids. The contents of guts from *S. quebecensis* and *Tipula* from Alik Lake and the tributary streams were examined microscopically. No differences were apparent and all guts contained about 95% detritus and 5% diatoms, filamentous algae and fungal hyphae. The fingernail clam, *Pisidium ventricosum* was the most ^{13}C depleted of the benthic invertebrate fauna of Alik Lake and had a mean $\delta^{13}C$ value similar to those of taxa collected from lotic habitats (-27.8‰).

Horizontal plankton tows at depths of 1–3 m and oblique tows from 10 m to the surface, failed to collect any invertebrates from Alik Lake during daylight. At night (23:30), however, the net clogged within 5 min when towed horizontally at low speed (3–5 km·h^{-1}). In decreasing order of abundance, the catches consisted of *Holopedium gibberum*, *Leptodiaptomus minutus*, *Heterocope septrionalis*, *Bosmina* spp., and an unidentified cyclopoid copepod, as well as small numbers of chironomid larvae and pupae. Samples of this plankton were also ^{13}C depleted compared with most of the benthic fauna of the lake (Fig. 3).

Mysids, eucarid shrimps (Natantia), and gammarid amphipods (mainly *Gammarus oceanicus*) dominated the catches in both the plankton and benthic dredge hauls from the Koroc estuary. These three taxa had mean $\delta^{13}C$ values of -19.9, -19.6, and -18.5‰, respectively (Fig. 3). Bivalve and gastropod (mostly *Littorina* sp.) molluscs were abundant on the blades of *Fucus* and *Laminaria*. The carbon isotope ratios of the bivalves were similar to those of the most ^{13}C enriched freshwater invertebrates, however, $\delta^{13}C$ values of the gastropods were considerably higher (Fig. 3).

Fish

The only species of fish observed in tributary streams were juvenile (3–10 cm total length (TL)) and adult (>30 cm TL) brook trout, and juvenile (3–12 cm TL) arctic char. Samples of all of these fish had $\delta^{13}C$ values similar to those of most of the invertebrates found within these habitats, though juvenile char were slightly more ^{13}C enriched than the brook trout (Fig. 4). Stable carbon isotope ratios of juvenile arctic char, and adult brook trout, lake trout, and sticklebacks from Alik Lake were very similar, and all were more ^{13}C enriched than fish from the

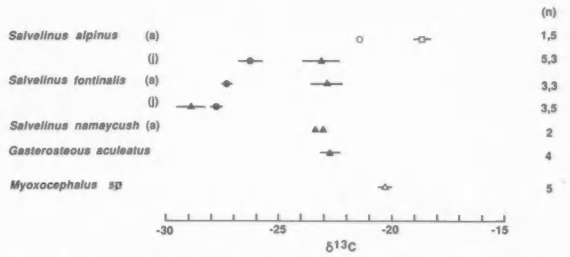

FIG. 4. Stable carbon isotope ratios ($\delta^{13}C$) of fish from the Koroc River system (mean ± 1SE, n = number of samples. Symbols as for Fig. 2; □ = Hulik Lake, winter 1985).

tributary streams. In contrast, three juvenile brook trout from the shallow littoral of Alik Lake were the most ^{13}C depleted of the fish sampled (Fig. 4).

Sculpins were the only fish collected from the Koroc estuary and had a mean $\delta^{13}C$ value of $-20.3‰$, similar to the samples of estuarine invertebrates. Adult arctic char, in particular those caught in early winter from Hulik Lake, were the most ^{13}C enriched of the fish collected from the Koroc system (Fig. 4).

Discussion

The utility of stable isotope tracing of energy flow in ecosystems depends on the existence of differences in isotope ratios among potential sources of energy available to consumers (Peterson and Fry 1987) but such variation is not always present. For example, Peterson et al. (1986) had little success with this technique in an Alaskan tundra stream because of the relative similarity of isotope ratios among different sources of organic matter. In the Koroc River system, however, terrestrial plants were isotopically distinct from aquatic macrophytes and both marine and freshwater algae. With the exception of samples collected from stones in the mainstem rapids, aquatic mosses were also more ^{13}C enriched than terrestrial vegetation, although only by about 2‰.

There was little evidence of epilithic algae in the small tributaries and mainstem rapids. Tundra streams have been shown to be nutrient limited and have a low primary productivity, despite ample insolation during summer (Peterson et al. 1985a; 1986). Although primary productivity was not measured in the Koroc system, the invertebrates from these habitats were generally too ^{13}C depleted to have derived a significant amount of energy from this source. Similarly, moss was too ^{13}C enriched to be the likely source of assimilated carbon because consumers generally have higher $\delta^{13}C$ values than their food (DeNiro and Epstein 1978; Peterson and Fry 1987). Terrestrial organic matter, particularly in the form of leaves shed from riparian trees and shrubs, seems to be the most likely source of energy fueling the invertebrate communities of lotic habitats in the Koroc.

The most notable exceptions among the invertebrates from lotic habitats were the simuliids and *S. quebecensis* collected from the headwaters of Aapic Creek. None of the samples of potential food materials collected in this study were sufficiently ^{13}C depleted to be a likely source of energy for these taxa. However, phytoplankton in the lake drained by this stream may well be sufficiently ^{13}C depleted (e.g. Rau 1978) to account for the low isotope ratios of the simuliids. Unfortunately, our samples of phytoplankton were insufficient for the analysis of stable carbon isotope ratios. Nymphs of *Siphlonurus* are known to be omnivorous (Edmunds 1960), so *S. quebecensis* may feed on blackfly larvae as well as on other materials exported from the lake.

In marked contrast to the small streams and rapids of the main river, the benthic fauna of Alik Lake did not appear to be as dependent on terrestrial sources of carbon. Moreover, despite its considerable biomass, the thick carpet of moss did not appear to contribute significantly to the energy pool. The preferential loss of ^{12}C during respiration usually results in the enrichment of consumer tissue relative to its food but only by about 1‰ (DeNiro and Epstein 1978). Most benthic taxa in the lake were about 3‰ more enriched in ^{13}C than the moss and, as a result, it is unlikely that this potential source of energy was being exploited to any great extent. The tissues of mosses seem to be especially refractory and are consumed by only a few species of freshwater invertebrates (Hynes 1970), even after they begin to decompose (Davies 1975; Welch 1976). The stable carbon isotope ratio of the small macrophyte, *Hippuris vulgaris*, was identical to that of several invertebrate taxa in the lake but is unlikely to be a major source of carbon because of its sparse distribution and abundance.

Epilithic algae were the most abundant ^{13}C enriched food source available to consumers in Alik Lake and may have contributed to the elevated $\delta^{13}C$ values of the benthic fauna. Algae could enter the food chain through grazing on stone surfaces in the euphotic zone of the lake as well as through sedimentation of epilithic algae that has been eroded from rocks upstream. As it settles, such material would be entrained by the thick bed of moss where dense populations of *Siphlonurus*, chironomids, and enchytraeid worms were recorded, the most ^{13}C enriched invertebrates in the lake.

There is also a possibility that marine sources of carbon are responsible for the ^{13}C enrichment of the fauna of Alik Lake. The rapids separating the lake from the level of spring high tides have a vertical drop of about 15 m, so direct tidal influx of seawater into the lake is unlikely. In addition, even though the deeper portions of the lake are below mean sea level, the benthic fauna consists of strictly freshwater taxa, including Tubificidae (*Rhyacodrilus* sp.), *P. ventricosum*, and Hydracarina. However, marine carbon may be introduced and incorporated into the food chains of the lake via the movements of arctic char. Both Alik and Hulik Lakes are major overwintering sites for arctic char in the Koroc River system (Boivin 1987). Adult char do not feed while in freshwater (Dutil 1986) from roughly September through mid-June, but do metabolize a large fraction of their lipid reserves accumulated while feeding at sea (Boivin 1987). Marine carbon may enter the freshwater food chain through respiration, as well as by the decomposition of fish that die during winter. Pacific salmon (*Oncorhynchus* spp.), which die shortly after spawning in freshwater streams, have been shown to make a significant contribution to the energy flow of rivers (e.g. Richey et al. 1975; Johnson and Ringler 1979). In contrast, arctic char are multiple spawners and postreproductive mortality may not be very great (Johnson 1980).

Clearly the benthic invertebrates of Alik Lake obtain their dietary carbon from at least two sources; most likely epilithic algae and terrestrial organic matter. However, we are unable to rule out possible contributions from aquatic moss, which has a considerable biomass in the lake, and marine sources. This problem of assessing the relative importance of several primary food resources may be resolved by the use of other stable isotopes, such as ^{15}N and ^{34}S, which can provide far greater resolution than the single carbon isotope tracer (Peterson et al.

1985b; Peterson and Fry 1987). Stable sulfur and nitrogen isotopes would be particularly useful in determining the contribution of marine sources of energy to food chains in the Koroc system. Unfortunately, our samples were insufficient to allow such determinations.

Fish in the small streams appeared to derive most of their energy from terrestrial sources via the benthic invertebrate fauna. It was apparent, however, that fish in Alik Lake did not derive all of their energy from feeding on the benthos, because their bodies were ^{13}C depleted compared with most invertebrates in the lake. They also must derive part of their energy from either plankton or drifting organisms from up-river, both of which had lower $\delta^{13}C$ values than the benthic fauna of the lake. The unusually low $\delta^{13}C$ values of juvenile brook trout from Alik Lake suggests that these fish have fed predominantly on plankton or perhaps simuliids or other ^{13}C depleted invertebrates from the tributary streams or rapids. Furthermore, the differences in $\delta^{13}C$ values between juvenile arctic char and juvenile brook trout in Alik Lake and the tributary streams also suggest partitioning of food resources in both habitats. Stenzel (1987) found that juvenile arctic char remain within restricted areas at least over short periods of time. Differences in $\delta^{13}C$ values of juvenile arctic char and juvenile and adult brook trout between Alik Lake and the tributary streams indicates that there is little movement of these fish within the Koroc system over the longer term.

Despite the potential export of dissolved and particulate organic matter from the river system (Peterson et al. 1986), terrestrial carbon does not appear to make a significant contribution to the estuarine food web. This may be a general feature of the nearshore communities of arctic embayments (Schell 1983). Of the estuarine invertebrates we sampled, only bivalves had $\delta^{13}C$ values indicative of a diet which may include detrital carbon carried by the river. However, these did not account for a large proportion of the estuarine invertebrate fauna and are rarely, if ever, eaten by arctic char. Mysids, shrimps, and amphipods, which are the most important invertebrate components of the diet of arctic char in the Koroc estuary (Adams 1987), had $\delta^{13}C$ values indicative of a dependence on marine sources of energy (Rounick and Winterbourn 1986). The high $\delta^{13}C$ values of adult char caught in the Koroc River confirm that these fish obtain most of their biomass carbon from feeding at sea.

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Biological Basis of Maturation and Spawning Waves in Pacific Herring (*Clupea harengus pallasi*)

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Ware, D. M., and R. W. Tanasichuk. 1989. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 46: 1776–1784.

Maturation rates (measured as the change in the gonosomatic index (GSI) with time) over the last month of the annual maturation cycle were estimated for male and female herring in British Columbia, between 1982–87. The data were analyzed to determine interannual and interregional differences in the maturation rate and its influence on spawning time. The data also indicated that in some areas herring spawned in discrete waves — the largest fish tended to spawn first and the smaller fish in subsequent waves. Each spawning wave lasted about 5–6 d and the interwave interval varied from 8–26 d in the Strait of Georgia. General equations were developed to describe gonadal growth over the entire maturation cycle. These equations accounted for the observed differences in: (1) the maturation rates between the sexes (males initially mature faster), (2) the interregional and interannual variation in the timing of spawning (herring tend to spawn later at higher latitudes, and earlier than normal when its warmer), and (3) provide an explanation for spawning waves. All of these phenomena derive from the fact that the instantaneous rate at which the gonad grows during the maturation cycle in both sexes depends on the weight of the fish, and the daily sea temperature.

On a estimé la vitesse de maturation (mesurée d'après la variation de l'indice gonosomatique (IGS) en fonction du temps) durant le dernier mois du cycle de maturation annuel chez des harengs mâles et femelles en Colombie-Britannique, de 1982 à 1987. On a analysé les données ainsi recueillies afin de voir si la vitesse de maturation diffère d'une année à l'autre et d'une région à l'autre et si elle influe sur l'époque de la fraye. L'analyse des données a aussi révélé que dans certaines zones, il y a des vagues de fraye séparées : les poissons les plus gros ont tendance à frayer en premier, puis les poissons plus petits suivent, par vagues. Chaque vague de fraye dure environ 5 ou 6 d et il s'écoule jusqu'à la suivante un intervalle variant de 8 à 26 d dans le détroit de Géorgie. On a formulé des équations générales pour décrire le développement gonadique durant le cycle de maturation. Ces équations mettent en jeu les différences observées aux points de vue suivants : 1) vitesse de maturation selon le sexe (la maturation des mâles est d'abord plus rapide), 2) variation d'une région à l'autre et d'une année à l'autre de l'époque de la fraye (le hareng a tendance à frayer plus tard aux latitudes plus élevées et plus tôt que la normale lorsque le temps est plus chaud) et 3) les équations apportent une explication de vagues de fraye. Tous ces phénomènes tiennent au fait que la vitesse instantanée à laquelle les gonades se développent durant le cycle de maturation, chez les deux sexes, dépend du poids du poisson et de la température journalière de la mer.

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Spawning in fishes is the culmination of a remarkable series of complex events. In British Columbian stocks of Pacific herring (*Clupea harengus pullasi*), spawning concludes a maturation process which begins 8 mo earlier in offshore waters, generally far removed from the spawning grounds, and includes migrating inshore to over-wintering grounds, homing to or near natal beaches, and synchronizing spawning readiness between the sexes (Hay 1985). It has been known for some time that although individual herring are total spawners, in the sense that they deposit all their eggs in 1–2 d, in some places herring spawn in discrete waves separated by several days, to several weeks. The largest, and oldest, fish in the stock tend to spawn in the first wave, with the smaller fish spawning in subsequent waves (Hay 1985). The timing of spawning also varies with temperature and latitude in B.C., the higher the temperature in the spring, the earlier the time of spawning (Hay 1985). The fact that spawning occurs later at higher latitudes may be due largely to the fact that the mean winter temperatures are colder at higher latitudes, so the herring take longer to reach full maturity. Hay (1985) points out, however, that there are some exceptions to this rule, so spawning is not just temperature dependent.

Since most of the herring caught in B.C. are taken in very intense fisheries just prior to spawning, it is important to learn how interannual variations in the maturation process and spawning time are affected by oceanic conditions, and other factors such as fish size. By understanding this process we will be in a better position to forecast when the stocks will reach full maturity, and can be harvested in different areas along the coast. Despite all the research that has been done on herring, surprisingly little is known about the factors influencing their maturation and spawning. Iles (1964) estimated the duration of maturity stages for various stocks of Atlantic herring (*Clupea harengus harengus*) and found that: (1) male and female North Shields herring appear to begin maturing simultaneously but the males mature more rapidly and reach stage V (final gonad size) earlier, (2) Manx herring of all ages mature at much the

same rate but the older fish began maturing earlier than younger fish, and (3) the rate of gonad growth does not differ markedly between northwestern North Sea stocks which mature simultaneously, but spawn at different times. Iles (1964) did not discuss the potential influence of the environment, nor the potential for interannual variations in maturation trends. In addition, describing maturation by using qualitative maturity stages is too subjective and could mask important changes which may be revealed by measuring gonad weight, and the gonosomatic index (GSI = percentage of the total fish weight accounted for by the gonad). Lambert (1987) presented analyses of the influences of sea temperature and fish size on spawning time of Atlantic herring in the Gulf of St. Lawrence, and of fish age on spawning in Norwegian herring. He concluded that temperature accounted for most of the variation in the average date of arrival on the spawning grounds and that, in both Gulf of St. Lawrence and Norwegian stocks, spawning time was negatively correlated with fish size, and age.

Hay and Outram (1981), and McGurk et al. (1980) measured seasonal variations in the herring GSI. Some questions which these studies do not resolve include: do females and males begin maturing at the same time, and does the gonad in both sexes grow at the same rate over the annual cycle? It also is not clear whether or not spawning occurs as soon as the fish reach full maturity. In some outer coast stocks in B.C., herring sometimes hold in a state of full maturity for several days to weeks before spawning, often near a neap tide (Hay 1989). In contrast, in more protected locations herring usually spawn as soon as they reach full maturity.

In our study of the maturation process in Pacific herring we posed the following questions: (1) to what extent is spawning time controlled by environmental factors like water temperature, and phenotypic characteristics such as body size? (2) how do the sexes synchronize spawning? and (3) what is the biological basis and significance of spawning waves?

Materials and Methods

Origin and Processing of Samples

Extensive information on the rate of increase of the GSI over the last month of the annual maturation cycle was obtained from roe test fishery samples collected at the major spawning areas in B.C., between 1982–87. The Canadian Department of Fisheries and Oceans charters commercial seiners annually to fish prespawning aggregations of herring and determine when the roe yield is high enough for a seine fishery. Frozen herring samples collected every 1–2 d are returned to the laboratory for routine biological determinations of standard length, total weight, sex, gonad weight, age, and maturity (modified Hjort scale (Hay 1985)). Since gonad weights were not measured routinely before 1982, our analysis was restricted to samples collected after that time, from major spawning areas which would have been sampled consistently within, and among seasons. These areas are shown in Fig. 1.

A database which consisted of the average total weight and GSI for all area, year, sex, date of collection, and maturity group combinations was developed. Although GSI is a good indicator of maturity (Iles 1964), it can be complicated by variations in fish weight. Ware (1985) found that the mature ovary weight (Q) is an increasing function of fish size. Therefore, fish of different sizes but the same GSI are at different levels of maturity; the smaller fish are more advanced.

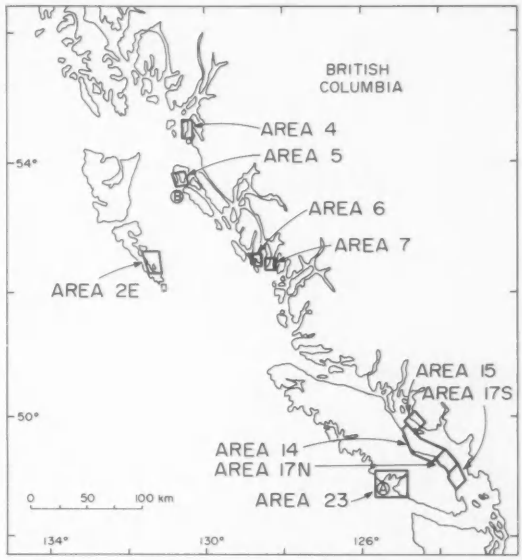

FIG. 1. Herring sampling locations. The enclosed areas indicate where major herring roe test fisheries occur. Note that Areas 14, 15, 17N and 17S are in the Strait of Georgia; Area 23 is Barkley Sound; Areas 6 and 7 are in the central coast; Area 2E is in the lower east coast of the Queen Charlotte Islands; and Areas 4 and 5 are in the north coast. The letters A and B indicate the locations of the Amphitrite Point and Bonilla Island lighthouses, respectively.

This size effect was removed in both sexes by estimating the difference between the expected value of Q and the observed GSI on the date of collection. Regressions relating Q to total body weight were estimated from the test fishery charter samples using data for 2244 males and 2629 females. Fish were sorted into maturity groups by generating frequency histograms of these differences. These distributions usually had just one or two distinct modes; each mode represented a separate maturity group which tended to spawn as a discrete wave. Regression analysis was used to statistically describe GSI maturation trajectories for all area, year, sex, and maturity group combinations. Simple and multiple linear regression equations, which examined the effect of time and average fish weight in each maturity group on the GSI trajectory, were tested. Results of an F-test recommended by Sokal and Rohlf (1981) indicated a significant ($p<0.05$) improvement in R^2 with the multiple regression which included both time and fish weight as independent variables; therefore the simple linear regression was abandoned.

Analysis of covariance (ANCOVA) and regression analysis were performed to test for the influence of fish size and sea temperature on the GSI trajectories. The ANCOVA tested for significant differences in parameter estimates for the slopes and adjusted means among maturity groups. Regression analysis was used to determine if significant differences in parameter estimates were related to fish weight and/or average sea temperatures 0–30, 30–60, and 60–90 d before spawning, when ovarian growth was most rapid (Tanasichuk and Ware 1987).

Early Maturation Stages

To describe how the GSI increases during the early stages of the annual cycle we reanalyzed the extensive data set collected

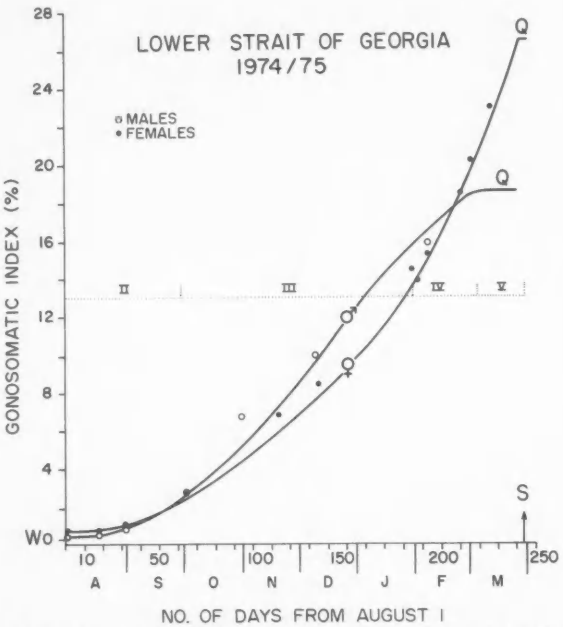

FIG. 2. Observed trend in the gonosomatic index of Area 17S male (open circles) and female (closed circles) herring, and modified Hjort maturity scale showing duration of stages II to V in females (after Hay et al. 1980 and Hay and Outram 1981). The plotted trajectories are for the grand mean weight of male (103 g) and female (125 g) herring in this maturity group. Wo indicates the starting GSI, and Q the GSI at full maturity. This particular wave of fish spawned on March 28 (Hourston 1980).

by Hay et al. (1980) in 1974–75. This study and one by McBride et al. (1959), which gives only monthly mean GSI values, represent the sole sources of fall and early winter GSI measurements for B.C. herring. Hay et al. (1980) collected fish from the lower Strait of Georgia (Area 17S; Fig. 1) on 27 occasions between July 30, 1974 and June 18, 1975. We reanalyzed the samples taken between July 30 and March 13, which covered the beginning of the annual cycle up to full maturity. Fish were assigned to maturity groups according to the procedure outlined above. Gonosomatic index-total body weight regressions were estimated for each sampling date, sex, and maturity group combination. Regressions based on sample sizes of less than 10 fish, or using data which did not represent the generally observed size range of 100–150 g were not used.

Results

Annual Maturation Cycle

Our reanalysis of Hay et al.'s (1980) data indicates that the size of the gonad when maturation begins differs significantly betwen the sexes. In females, the GSI starts increasing at the end of July from a resting value of 0.52%, which is independent of body weight. Males begin maturing in mid-August at a starting GSI of 0.47%, which is also independent of body weight. Consequently, the male "gametogenesis clock" appears to start running about 2 wk later than the female's. Once maturation begins, the GSI at any time up to spawning is an increasing function of body size in both sexes. This observation establishes that larger herring mature faster in B.C.

TABLE 1. Ovary maturation regression coefficients for Strait of Georgia herring (1982–87), mean female weight (W), K the rate constant, B the weight dependent coefficient, and Q the average GSI at full maturity. The data were fitted to the model: $GSI = KT + BW + C$, where T = time in days from an arbitrary starting date (Feb. 9) and C = intercept. NS = not significant. Area 14 = Upper Strait; Area 15 = NE Strait; Area 17N = North Central Strait; Area 17S = Lower Strait (Fig. 1).

		Model					
Area	Year	N	R^2	K (%/d)	B (%/g)	W (g)	Q (%)
14	82	5	0.983	0.348	0.089	127	26.5
15	82	6	0.784	(0.844)[a]	NS	118	26.1
17N	82	7	0.831	0.303	0.073	90	24.5
17S	82	10	0.725	0.357	0.077	114	25.8
			Means	0.336	0.080	112	25.7
14	83	20	0.832	0.582	0.169	131	26.7
15	83	39	0.576	0.339	0.161	110	25.6
17N[b]	83	19	0.764	0.315	0.150	116	26.0
17S	83	7	0.977	0.333	0.161	122	26.2
			Means	0.392	0.160	120	26.1
14	84	8	0.918	0.411	NS	127	26.5
15	84	16	0.811	0.342	0.086	105	25.4
17N	84	12	0.900	0.253	0.091	104	25.3
17S	84	18	0.928	0.289	0.076	116	26.0
			Means	0.324	0.084	113	25.8
14(1)	85	15	0.49	0.301	0.05	117	26.0
14(2)	85	13	0.92	0.255	0.12	83	24.0
15	85	13	0.68	0.286	0.14	86	24.2
17S	85	8	0.96	0.350	0.08	122	26.3
			Means	0.300	0.097	102	25.1
14[c]	86	29	0.82	0.315	0.128	102	25.2
15	86	8	0.86	0.412	NS	100	25.1
17S	86	8	0.97	0.454	NS	101	25.2
			Means	0.394	0.128	102	25.2
14[c]	87	25	0.65	0.248	0.083	113	25.8
15	87	18	0.92	0.385	0.082	110	25.6
17S	87	18	0.77	0.341	0.054	94	24.7
			Means	0.325	0.073	106	25.4

[a]Unusually high value; probably an artifact caused by combining fish from two different maturity groups.

[b]Majority of fish spawned in Area 14.

[c]Area 17N samples were grouped with Area 14 because they were in the same state of maturity.

During the first 6 mo of the annual cycle, Hay et al.'s data indicate that the GSI of males is higher than it is for females (Fig. 2). By the seventh month (February in southern B.C.), the GSI's of both sexes are equal. McBride et al. (1959; their table 1) present similar results; their measurements unequivocally confirm that males have higher GSI's than females from September to February, inclusive.

In the last month before spawning the GSI increases rapidly in females and surpasses that of the males. A multiple regression analysis of the Strait of Georgia roe test fishery data (1982–87), collected in February and early March, reveals that the male GSI increases at an average rate of 0.14%/d, which is about half the rate (0.34%/d) estimated for females from the same samples (Tables 1 and 2). We obtained similar rates from an ANCOVA of the roe test fishery samples from other areas in the last month before spawning (coast-wide average for males = 0.12%/d, for females = 0.33%/d). The coast-wide equation for males was: $GSI = 0.12 \cdot T + 0.07 \cdot W + C$ ($n = 29$

TABLE 2. Testicular maturation regression coefficients for Strait of Georgia herring (1982–1987), mean male weight (W), K the rate constant, B the weight-dependent coefficient, Q the average GSI at full maturity, and H the occurrence of holding: N = no holding, Y = apparent holding, number of days in parentheses. The estimates are based on frozen fish: NS = not significant; NT = no trend; the Area 17N samples were grouped with Area 14.

		Model						
Area	Year	N	R^2	K (%/d)	B (%/g)	W (g)	Q (%)	H
14	82	10	0.82	0.21	0.07	101	18.6	N
15	82	5	0.99	(0.65)[a]	NS	104	18.8	N
17S	82	8	0.83	0.20	NS	108	19.1	N
		Means		0.20	0.07	104	18.8	
14	83	9	0.26	NT	NT	113	19.4	Y(3)
15	83	33	0.61	0.13	0.11	101	18.6	N
17S	83	11	0.74	0.16	0.11	103	18.7	N
		Means		0.14	0.11	106	18.9	
14(1)	84	15	0.87	0.12	0.07	110	19.2	N
14(2)	84	5	0.94	NS	0.12	88	17.5	N
15	84	17	0.78	0.08	0.10	91	17.0	N
17S	84	11	0.88	0.18	0.09	96	18.2	N
		Means		0.13	0.09	96	18.0	
14	85	38	0.21	NT	NT	85	—	Y(9)
15	85	12	0.55	NS	0.11	77	16.6	N
17S	85	11	0.93	0.19	0.10	91	17.8	
		Means		0.19	0.10	84	17.2	
14	86	36	0.62	0.20	0.07	92	18.5	N
15	86	12	0.64	NS	NS	90	17.7	Y(22)
17S	86	11	0.79	0.07	0.09	86	17.4	N
		Means		0.13	0.08	90	17.9	
14	87	23	0.76	0.08	0.09	101	18.6	N
15	87	19	0.46	0.12	0.09	100	18.5	N
17S	87	12	0.91	0.14	0.09	82	17.0	Y(4)
		Means		0.11	0.09	94	18.0	

[a]Unusually high value; probably an artifact caused by combining fish from two different maturity groups.

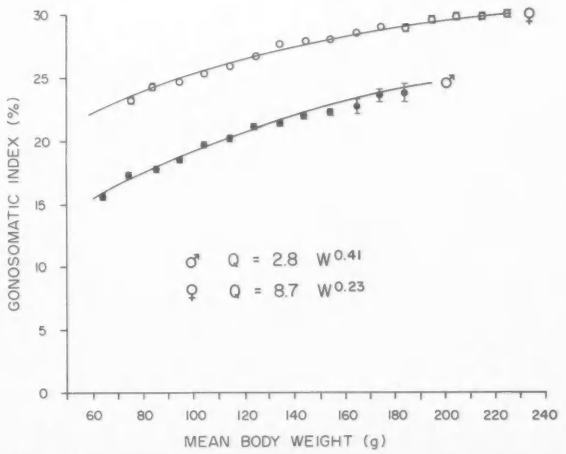

FIG. 3. Relationship between gonosomatic index at full maturity (Q) and body weight in British Columbia stocks of Pacific herring. The equations describing the fitted curves apply coastwide. The 95% confidence limits are shown.

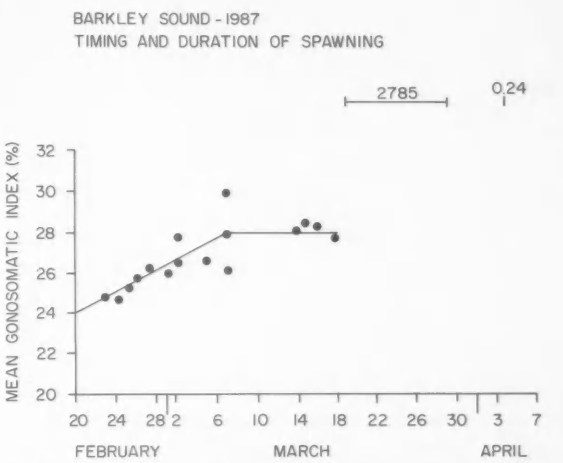

FIG. 4. An example of holding by Barkley Sound female herring. The maturation trajectory indicates that this wave reached full maturity about March 7, and then held in that state until March 18 when spawning began. The horizontal bars at the top of the figure indicate when spawning commenced and ended, and the thousands of square metres of spawn deposited. Note that a small second wave spawned on April 4.

TABLE 3. Occurrence of B.C. herring stocks holding at full maturity, 1982–87. The denominators in the occurrence column indicate the number of maturity groups examined for evidence of holding.

	Males		Females	
		Days held		Days held
Location	Occurrence	($\bar{x} \pm s$)	Occurrence	($\bar{x} \pm s$)
Area 14	1/8	3	0/11	0
Area 15	2/6	15 ± 9.2	0/6	0
Area 17S	1/6	4	0/10	0
Area 23	4/8	15 ± 5.3	4/7	11 ± 3.6
Area 6, 7	2/9	17 ± 13.4	0/11	0
Area 4, 5	7/8	17 ± 9.4	1/9	5
Area 2E	3/4	7 ± 2.5	3/5	15 ± 10.1
Total	20/49		8/59	

maturity group means; $r = 0.93$; $p < 0.0001$), and for females: $GSI = 0.33 \cdot T + 0.07 \cdot W + C$ ($n = 51$ maturity group means; $r = 0.95$; $p < 0.0001$), where T = time in days from an arbitrary starting date (Feb. 9), and W = average body weight of each sex. An analysis of the weight-adjusted group mean GSI's in females along the coast indicates that these values are positively correlated with the average sea temperature over the last 90 d before spawning ($n = 51$ maturity group means; $r = 0.53$; $p < 0.0001$). The $Q10$ estimated from this relationship (2.4) is within the expected range of two to three for physiological processes (Hoar 1966). This finding demonstrates that the maturation rate is also temperature, as well as size dependent.

At full maturity the GSI (Q) for females is about six percentage points higher than it is for the same sized male (Fig. 3). Results of an ANCOVA of the coastwide data indicates that the slopes of the Q-total body weight regressions are significantly different between the sexes ($p < 0.05$).

Male herring tend to reach full maturity (Q) and hold in this state more frequently than females. In most places in B.C. female herring spawn as soon as they reach full maturity.

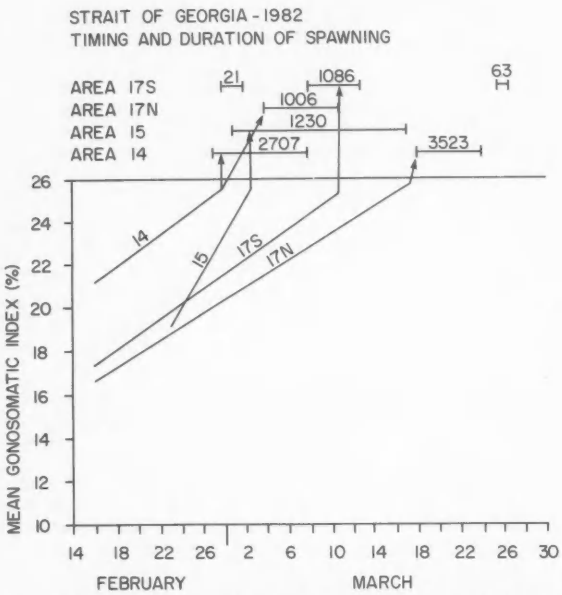

FIG. 5. Spawning waves and maturation trajectories of female herring in different statistical areas in the Strait of Georgia, 1982. The trajectories shown here are from the multiple regressions given in Table 1 for the average female body weight in each area. The horizontal bars at the top of the figure indicate when spawning commenced and ended, and the thousands of square metres of spawn deposited. The arrows indicate where each wave of fish is believed to have spawned. There are some minor movements of fish between adjacent Areas like 17N and 14. Note that more than one wave of fish spawned in Areas 14 and 17S.

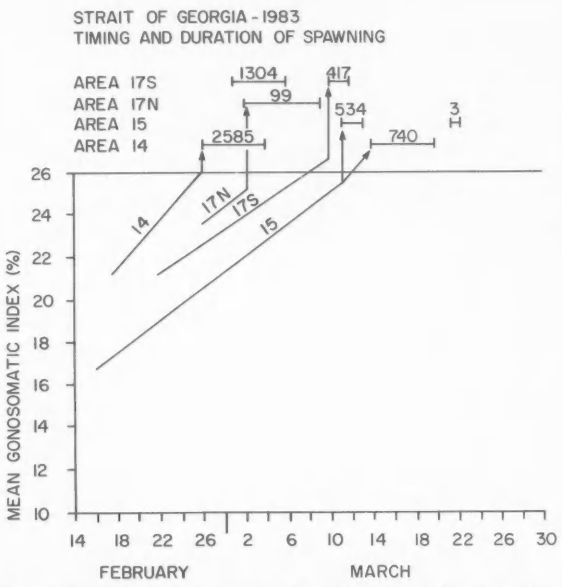

FIG. 6. Spawning waves and maturation trajectories of female herring in different statistical areas in the Strait of Georgia, 1983 (from multiple regressions listed in Table 1). Part of the body of fish in Area 15 may have moved to Area 14 to spawn. Note that two waves of fish spawned in Areas 14, 15, and 17S.

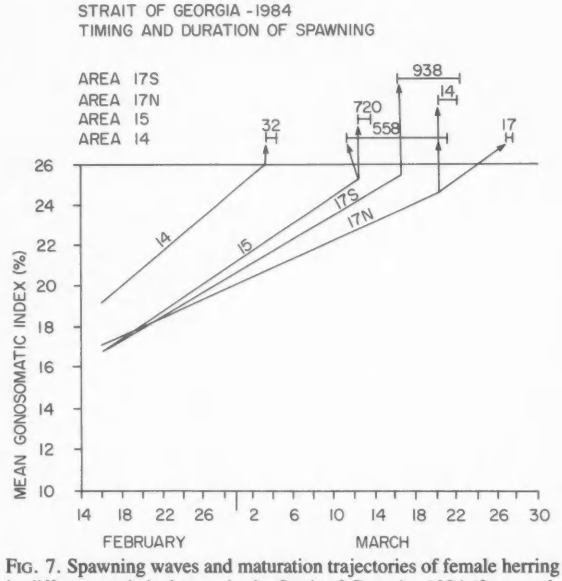

FIG. 7. Spawning waves and maturation trajectories of female herring in different statistical areas in the Strait of Georgia, 1984 (from multiple regressions listed in Table 1). Note that three waves of fish spawned in Area 14. Part of the bodies of fish in Areas 15 and 17N may have moved to Area 14 to spawn.

However, two notable exceptions occur in Barkley Sound (Area 23) and Juan Perez Sound/Skincuttle Inlet (Area 2E). Here, spawning appears to be influenced by the tides, and usually occurs within 3 d of the neap tide. Events in 1987 showed that the main spawning wave in Barkley Sound reached full maturity (Q) near the neap tide on March 9 and then held at this stage for approximately 9 d, before spawning near the next neap tide on March 21 (Fig. 4). In contrast, there is ample evidence of males holding for a few days, to weeks, before spawning. Our analysis of the coast-wide roe test fishery data indicated that males held in 20 of the 49 maturity groups examined (Table 3). Holding was also evident along the entire coast. In contrast, in females there was evidence of holding in only eight of 59 maturity groups examined (Table 3); seven of eight instances of holding occurred at outer coast locations (i.e. Areas 2E and 23), where spawning time has been found to be weakly linked to the tidal cycle (Hay 1989).

Evidence for Spawning Waves

In some areas more than one maturity group, or wave, of herring spawns during the same season. Although this phenomenon has been recognized for decades, the amount of interannual variability has not been documented. Hay (1985) presented some evidence for wave spawning in Barkley Sound in 1982, but did not indicate how extensive the phenomenon was, nor how frequently it occurred. The largest GSI data set in B.C. is for the Strait of Georgia, between 1982–85. The resulting GSI trajectories for an average sized female, and the observed timing and duration of spawning in each statistical area are summarized for those years in Figs. 5–8. Inspection of these figures indicates that two or three waves of herring usually spawn around Lambert Channel (Area 14) and sometimes in the lower Strait of Georgia (Area 17S). The interwave interval (difference

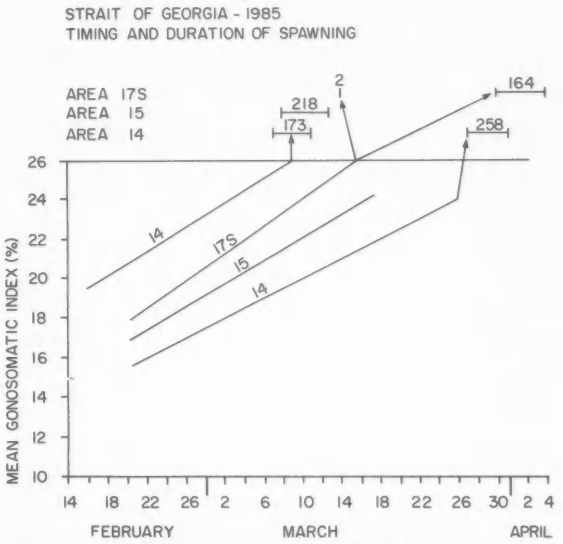

FIG. 8. Spawning waves and maturation trajectories of female herring in different statistical areas in the Strait of Georgia, 1985 (the trajectories are from the multiple regressions listed in Table 1). Note that two waves of fish spawned in Area 14. Part of the body of fish in Area 17S may have spawned on March 13, the rest may have held and then spawned on March 29. It is not clear where the body of fish being tracked in Area 15 spawned. It may have moved to Area 14, and spawned there in the second wave.

between starting dates) varied from 8–26 d (average = 16 d), and smaller females spawned in the second wave (Table 4). The average duration of the spawning waves was 5–6 d. In a longer term context, between 1942–79 the first wave spawned in Area 14, on average, on March 10 (calendar day 69, Hourston 1980). Since the inter-wave interval was about 16 d, this meant that the second wave spawned on average about March 26 (calendar day 85). In Area 14, the first wave has spawned as early as Feb. 11 (1963) and as late as April 4 (1945) (Hourston 1980).

Interannual and Interregional Variation in Spawning Time

Generally the warmer the temperature, or lower the latitude, the earlier the maturation and spawning time (Hay 1985). These tendencies are apparent in Fig. 9, which summarizes the date of first spawning along the B.C. coast from 1982–87. The results show that spawning normally begins earlier (March 6 ± 6 d, on average) in the south coast (Area 14), starts about 15 d later (March 21 ± 9 d) in the central coast (Area 6), and about 30 d later (April 5 ± 4 d) in the north coast (Areas 4 and 5). The Barkley Sound stock (Area 23) forms an exception to this rule, since it has spawned relatively late in some years, for example 1985. However, this is also one area where the females sometimes hold in a state of full maturity for several weeks before spawning (Table 3).

With respect to temperature, there is a clear correlation (Table 4) between the average December to February temperature and the appearance of the first spawning waves in Area 14 (Chrome Island sea surface temperature (SST); $r = -0.94$ $p<0.01$). In Area 17S, though the correlation has the correct sign, the data are more variable and the correlation is not significant (Entrance Island SST; $r = -0.65$; $p>0.05$). Note that without exception temperatures were consistently cooler each spring, and spawning consistently later in Area 17S. This tendency is also apparent in Fig. 9, in the sense that spawning was latest coastwide in 1985, which was the coldest year in the series, and earliest in 1983, which was the warmest year. Although spawning time is affected by temperature, it cannot account for all the interannual and interregional variation. Evidently other factors like fish size are also important.

Modelling the Maturation Process

Guided by what we know about the annual maturation cycle in herring, we developed a model of this process, which explicitly considers the effects of body weight and sea temperature on the maturation trajectory, and the time both sexes require to reach full maturity (Q). In accordance with the observed GSI maturation curves (Fig. 2), the process we envisage for females assumes that the ovary, relative to the body weight, starts growing exponentially at the end of July at an instantaneous rate (k), which is an increasing function of the body weight (W) and the ambient water temperature (S):

$$(1) \qquad dG/dT = kG = AS^B W^D G,$$

where G-gonosomatic index. The process we envisage for males has the same structure, but to explain the unusual shape of the male GSI maturation curve (Fig. 2), we needed to introduce a

TABLE 4. Timing of spawning of first and second waves in Areas 14 and 17S (Strait of Georgia). The mean body weight of the females in each wave, the interwave interval and the mean sea surface temperatures (over the last 3 mo before spawning) are also shown for each area. SST = sea surface temperature.

Area	Year	Starting dates		Mean weight (g)		Inter-wave interval (d)	Mean SST (°C)
		Wave 1	Wave 2	Wave 1	Wave 2		
14	1982	Feb. 28	Mar. 19	117	90	19	8.1
14	1983	Feb. 26	Mar. 14	131	110	16	8.7
14	1984	Mar. 4	Mar. 12	127	105	8	8.0
14	1985	Mar. 7	Mar. 27	117	83	20	7.5
14	1986	Mar. 9	None	102	—	—	7.5
14	1987	Mar. 5	Mar. 18	117	104	13	7.9
17S	1982	Mar. 7	Mar. 26	114	—	19	7.4
17S	1983	Mar. 1	Mar. 10	122	—	9	7.8
17S	1985	Mar. 14	Mar. 28	122	—	14	7.2
17S	1986	Mar. 15	Apr. 10	101	—	26	7.3
17S	1987	Mar. 13	Apr. 4	94	—	22	7.7

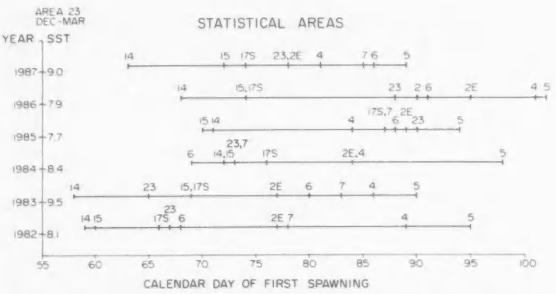

FIG. 9. Timing of spawning by the first wave in the major statistical areas in B.C. from 1982–87. The average sea surface temperature from Dec.–Mar. at Amphitrite Pt. lighthouse in Barkley Sound is also shown, and indicates that 1983 was the warmest winter, and 1985 the coldest winter, in this series along the coast.

"time-dependent brake" to slow the rate at which the GSI advanced in the last 3 mo of the cycle:

$$(2)\quad dG/dT = kG = AS\,W^{B}\,T^{C}\,G^{-D},$$

where T indicates the time in days since maturation began.

GSI maturation trajectories were obtained by numerically integrating equations (1) and (2), using daily sea surface temperature data and the average body weight of the fish in each spawning wave, as input. The best fitting estimates of A, C, and D in these equations were determined by choosing trial values for each sex so the resulting GSI maturation trajectories for Area 14 matched: (1) the shape of the observed GSI curves, (2) the average date of spawning by the first wave of spawners (age 4 and older), (3) the average date of spawning by the second wave of recruit spawners (age 3), and (4) the variation in spawning time between warm and cold years. Since our statistical analysis of the roe test fishery data showed that the female GSI maturation $Q10$ was about 2.4, we estimated that $B = 0.93$. The relevant input data used in the simulations, and the estimated parameter values for each sex that provided an acceptable match to the empirical data are summarized in Table 5.

Our analysis of simulated GSI trajectories suggests that males probably have a lower $Q10$ (approximately 2.1) than females. Since the rate at which the male GSI advances is quite different from the pattern in females (Fig. 2), we found that spawning would not be synchronized in cold years unless the $Q10$'s differ between the sexes (Fig. 10). Assuming this is true, the simulated trajectories in Fig. 10 show that males tend to mature about 4 d earlier than females in warm years, 2 d in normal years, and mature almost synchronously with the females in cold years. These results imply that our hypothesis that the male $Q10$ is lower can be tested in the future by determining if the difference between the dates when each sex reaches full maturity is positively correlated with water temperature.

Application

Simulated Interregional and Interannual Variability in Spawning Time

To determine how well the general model can explain interannual variability in spawning time in other regions, we computed maturation trajectories for the north coast stock (Areas 4 and 5) for the years 1982–87, and compared them with the observed spawning times. For these simulations we used sea surface temperature data from the Bonilla Island lighthouse (near overwintering and summer feeding areas for north coast herring; Fig. 1), and the female maturation characteristics listed in Table 5 for Area 14 fish (i.e. starting GSI, starting date, $Q10$, and parameter values A, B, and C). The average body weights (W, and corresponding values of Q) of females in the first spawning wave in the north coast, in each year, were obtained from the roe test fishery data.

For the period in question the simulations indicate that north coast herring reach full maturity on March 28, on average (Table 6). The generally good agreement between the observed and expected dates (the two dates are not significantly different; $t = 0.52$, $p > 0.5$) provides independent confirmation that: (1) much of the interannual variation in the time it takes herring to reach full maturity is associated with local temperatures and average body size of fish in the spawning wave; and (2) the parameter values describing the maturation process in the south coast (Table 5) also apply to the north coast. An average error of 8 d between the observed and expected dates of spawning is remarkably close, considering that we are simulating a process that lasts 8–9 mo.

Discussion

Our results show that maturation, and the timing of events associated with this process, are very different in male and

TABLE 5. Comparison of maturation characteristics of male and female Pacific herring in upper Strait of Georgia (Area 14).

Variable	Females	Males
Mean body weight (g)	125	103
Starting GSI (%)	0.52	0.47
Starting date	July 31 (day 212)	Aug 15 (day 227)
$Q10$	2.4	2.0–2.1
Terminal maturation rate (%/d)	0.33	0.12
Mean date at full maturity	March 10 (day 434)	March 8 (day 432)
GSI at full maturity (%)	26.4	18.7
Maturation parameters		
A	9.46×10^{-4}	2150
B	0.93	0.78
C	0.17	0.17
D	0	2.5

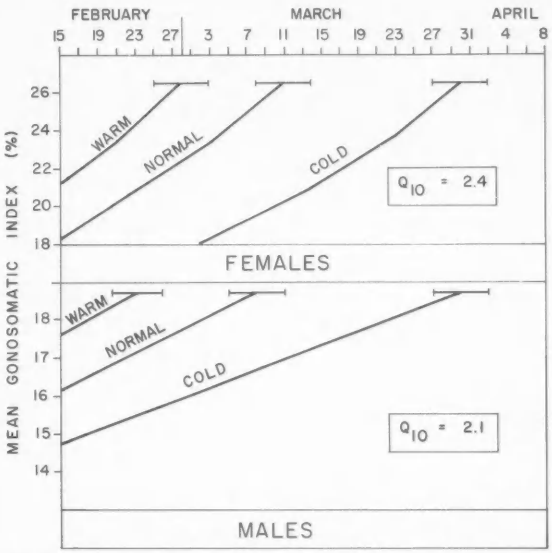

FIG. 10. Simulated maturation trajectories of the first spawning wave in Area 14 in warm, normal, and cold years. Note that the male $Q10$ has to be slightly less than the female $Q10$ for spawning to be synchronized. If both sexes have the same $Q10$ (2.4) males will mature about a week later than females in a cold year.

female herring. In B.C. stocks testicular growth begins several weeks later than ovarian growth; the testes grow at a maximum rate for roughly 5 mo before spawning, whereas the ovarian growth rate increases steadily with time and reaches a maximum (0.33%/d) in the final stages of the cycle. In addition, both the starting and terminal GSI's are significantly different between the sexes.

In view of these dissimilarities, how is spawning synchronized? Our simulation analysis suggests that this is mediated by the observed variation in body size between the sexes, and the postulated difference in $Q10$'s. The smaller body size of the males, coupled with the lower $Q10$ (Table 5), insures that they reach full maturity and hold in this state a few days to a week before the females in the same spawning wave mature. The striking difference in the frequency and duration of holding between the sexes suggests that the females ultimately determine the timing of spawning. Although this act appears to be initiated by the release of milt (Hay 1985), females may control spawning by using the pheromonal mechanism described by Dulka et al. (1987) for goldfish (*Carassius auratus*). These authors concluded that the release of 17-alpha,20-beta,dihydroxy-4-pregnen-3-one (17,20P), the proposed oocyte maturation-inducing steroid hormone in goldfish and other teleosts, synchronizes milt production with ovulation. Stacey and Sorenson (1986) reported that 17,20P is one of the three reproductive pheromones released by goldfish. A metabolite of 17-beta estradiol or substances released under estrogenic stimulation may signal the gender of the females. 17,20P, which is released at maximal levels by females in the process of final oocyte maturation, has a stimulatory effect on milt production. Stacey and Sorenson (1986) stated that females appear to release a third pheromone which acts as a "releaser" to male spawning behaviour. Although it seems reasonable that the first and third pheromones may also be released by Pacific herring, the action

TABLE 6. Observed spawning time of north coast herring and the expected times estimated from equation (1). W = average female body weight (g); PS = Port Simpson spawning; K = Kitkatla Inlet spawning.

			Calendar day of first spawning		
Year	W	Q	Observed	Expected	Error
1982	116	26.8	86(PS)	80	−6
1983	131	27.7	86(PS)	82	−4
1984	116	26.8	82(PS)	74	−8
1985	114	26.6	94(K)	89	−5
1986	156	29.2	101(PS)	116	+15
1987	126	27.4	92(K)	79	−13
		Average	90	87	8

of 17,20P may be somewhat different. Since male herring have attained their maximum GSI (Q) before spawning begins, 17,20P does not appear to act by increasing milt volume, otherwise the GSI would increase just prior to spawning. It is also consistently observed that females do not spawn until the males are running ripe. Therefore, in Pacific herring 17,20P may act by stimulating the onset of the process which leads directly to milt release; this, in turn, triggers spawning in females. Recent work (Ohtake et al. 1987) supports the suggestion of a pheromonal influence of females on males. These authors found that a substance, released from herring eggs, increased sperm motility.

Our analysis of simulated GSI trajectories shows that the combined influence of water temperature and body size on the maturation rate is sufficient to explain: (1) much of the interannual variation in spawning time at a given location, (2) much of the interregional variation in spawning time, and (3) why herring spawn in waves. The results indicate that the maturation rate is influenced by temperature, and imply that this effect is progressively greater later in the cycle in females, because the ovary grows exponentially. Therefore, the relationship between spawning time and temperature that Hay (1985) describes is a consequence of the influence of temperature on the maturation rate of females, as is the consistent observation that spawning time for B.C. herring increases progressively up the coast every spring (Fig. 9). Lambert (1987) describes a similar relationship between temperature and mean date of arrival for Gulf of St. Lawrence herring. Although he felt that temperature was the most important factor, he was unable to evaluate it's effect on the onset of maturation or how it affected the maturation rate. According to our model equation (1) the influence of temperature on the date of full maturity in females can be described by: $\text{day} = 177 - 13.7{*}t$, where t = average sea surface temperature (°C) over the last 90 d of the cycle. The date of full maturity also depends on the size composition of the stock and can be described by: $\text{day} = 103 - 0.256 \cdot W$, where W = average female weight (grams). These relationships imply that a 1 degree change in temperature has the same effect on the timing of full maturity as a 55-g difference in average weight.

Cushing (1975) proposed that the timing of spawning is important in determining the early survival of herring because the larvae must hatch at an appropriate point in the spring production cycle to find sufficient food resources. This hypothesis may explain why Pacific herring over-wintering areas are close to the spawning grounds, and why herring arrive there at least 3 mo before spawning. By arriving early, the trade-off in egg size and fecundity that is occurring in the ovary at this stage of the cycle (late stage III and stage IV; see Tanasichuk and Ware

1987) will be regulated by oceanic conditions in the area where the larvae will be born. Thus Tanasichuk and Ware (1987) found that in a warm spring, when spawning is early, egg size is smaller than average and fecundity higher than average. This trade-off presumably offsets the tendency for the mortality/growth rate ratio to be higher than normal when its warm. Conversely, in a cold spring when spawning is delayed, egg size is larger and fecundity lower, than average. This will be adaptive if the mortality/growth rate ratio also tends to be lower than normal in a cold spring, either due to a relaxation of the egg and larval mortality rate, or an enhanced growth rate (Tanasichuk and Ware 1987).

The model we developed to describe the maturation process in herring suggests that the phenomenon of wave spawning is determined by the difference in size-at-age and by the fact that the instantaneous maturation rate (k) is size dependent. We found that all sizes of Pacific herring start maturing at the same time, but the larger ones mature faster. We also found, as did Hay (1985) and Lambert (1987), that larger herring spawn earlier. Lambert attributed the resulting progressive decline in fish size over time to the effect of age, which is consistent with our findings since herring size and age are strongly correlated. Simulation results for the Strait of Georgia, using equations (1) and (2), indicate that 7 and 8-yr old herring (averaging 159 g) should reach full maturity and spawn about 4 d earlier than age 5 and 6 herring (averaging 143 g), and 15 d earlier than age 3 and 4 herring (averaging 104 g). This implies that in Areas 14 and 17S the oldest females in the stock down to, and including, some large 4-yr olds probably spawn in the first wave, while small 4-yr olds and age 3 recruit spawners probably spawn in the second wave, 16 or so days later. According to this mechanism, the size composition of the stock will determine how spawn is distributed over time, and the inter-wave interval. In the Strait of Georgia we can expect anywhere from one to three spawning waves in some areas. In general, spawning should be protracted in years when the size range of the stock is large.

It has been recognized for some time that wave spawning results in a succession of larval cohorts (Hourston 1958; Ware and Henriksen 1978; Lambert et al. 1982; Hay 1985); it is less widely appreciated that this succession of cohorts may be a "bet-hedging" strategy to offset natural vicissitudes during the early life history. Lambert (1987) cites a number of reasons why herring recruitment may be enhanced when spawning is distributed more broadly in time and space. Perhaps most importantly he notes that herring often spawn during unsettled weather in the spring and late autumn, and that the total egg production of the stock should be less vulnerable to storm damage when eggs are deposited in discrete waves over time. It also occurs to us that ocean climate tends to be cyclical in the sense that runs of above average temperatures are often followed by runs of below average temperatures that are equivalent to, or longer, than the expected reproductive lifespan of an individual. Consequently, as a herring ages, the maturation process we outlined above ensures that it spawns progressively earlier in relation to the secondary production cycle. Again, because of interannual uncertainties in the food supply, predation pressure, and possible density-dependent interactions within a year-class, wave spawning may enhance an individual's fitness over its reproductive lifespan.

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A Conceptual Model for the Estimation of the Sensitivity of Black Fly Larvae to *Bacillus thuringiensis* var. *israelensis*

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Results from bioassays of a commercial formulation of *Bacillus thuringiensis* var. *israelensis* (Teknar HP-D) are combined with an empirical model of the feeding rate of larvae of a target species of black fly (*Simulium venustum/verecundum*) to develop a model relating the mortality of larvae to the amount of formulation ingested per unit mass of larvae (specific ingested dose). LD_{50} of Teknar HP-D was about 1 μg wet mass of Teknar per milligram dry mass of larvae, and independent of size of the larvae and seston concentration. Compared with standard assay analysis relating the mortality to the dose (milligrams per litre times seconds), the proposed model allowed more precise and replicable estimation of the effective dose. Reanalysis of published data on the potency of another Bti formulation (Teknar WDC), confirmed the superiority of the proposed model over the standard procedure. Susceptibility of larvae to particulate larvicides is mainly a function of the larval feeding rate. In addition to size of the larvae, temperature, and seston concentration, analysis of the model reveals that the length of the contact period and the variability of feeding rates among individual larvae are important factors determining the mortality rate following treatments.

Les auteurs regroupent les résultats de bio-analyses d'une préparation commerciale de *Bacillus thuringiensis* v. *israelensis* (Teknar HP-D) et ceux d'un modèle empirique du taux d'ingestion de larves d'une espèce cible de moucheron (*Simulium venustum/verecundum*) afin d'élaborer un modèle établissant un rapport entre le taux de mortalité des larves et la quantité de préparation ingérée par unité de masse de larves (dose ingérée spécifique). La DL_{50} du Teknar-D se situe à environ 1 μg de Teknar (masse humide) par milligramme de larves (masse sèche) et est indépendante de la taille des larves et de la concentration du seston. Par rapport à l'analyse type établissant un lien entre le taux de mortalité et la dose (mg/L × s), le modèle présenté permet d'obtenir une estimation de la dose efficace plus précise et facile à répéter. Une analyse susbéquente de données publiées sur l'efficacité d'une autre préparation de Bti (Teknar WDC) confirme la supériorité du modèle présenté par rapport à la procédure type. La sensibilité des larves aux larvicides solides est surtout fonction du taux d'ingestion. En plus de la taille des larves, de la température et de la concentration du seston, l'analyse du modèle révèle que la durée de la période de contact et la variabilité des taux d'ingestion de chaque larve sont d'importants facteurs qui influent sur le taux de mortalité suite aux traitements.

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Commercial formulations of the larvicide *Bacillus thuringiensis* var. *israelensis* (Bti) are increasingly used around the globe to control black flies (Undeen et al. 1981; Chilcott et al. 1983; Gaugler et al. 1983; Colbo and O'Brien 1984; Olejnicek et al 1985a,b; Kurtak et al. 1987). Several factors favour Bti over chemical larvicides: biodegradability, high specificity, and efficacy in both cold and warm waters. However, the apparent potency of Bti varies greatly with seston load, and the size and species of the larvae (Lacey et al. 1978; Lacey and Undeen 1986, 1987). This large variability detracts from Bti as an alternative to standard chemical larvicides because the efficacy of control programs depends on adequate knowledge of the susceptibility of larvae. Models that predict the susceptibility of larvae in various conditions could help reduce the cost of assays and improve the efficiency of control programs.

Susceptibility of larvae to various larvicides is determined empirically from laboratory or field assays. In standard assays (Lacey et al. 1982; Undeen and Lacey 1982), groups of larvae are exposed to increasing concentrations of larvicide for a fixed

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period of time, and the observed mortality rate is regressed against the concentration of larvicide to determine the effective dose. However, like most other larvicides used to control black flies, Bti has to be ingested to be toxic (Lacey and Federici 1979). Thus, the larval mortality should vary as a function of the amount of Bti actually ingested. Standard assays imply that ingestion of Bti is simply a function of larvicide concentration and the contact time, and is independent of other factors (such as temperature, food concentration, or larval size), an assumption contradicted by observations on feeding rates of black fly larvae (Elsen and Hébrard 1979; Elsen 1980; Hart and Latta 1985; Kurtak 1978; Lacey and Mulla 1975; Walsh 1985).

In this paper we argue that the apparent variability in the potency of Bti formulations when used in different conditions can be explained in large part by the larval feeding rate. Here we report the mortality rates of *Simulium venustum/verecundum* larvae when exposed to a commercial formulation of Bti under various conditions. Bioassay results are first analyzed by the standard procedure. Then, using an empirical model of *S. venustum/verecundum* feeding rate (Morin et al. 1988b), we develop and test a model relating mortality rate to the specific ingested dose of Bti.

Methods

Experimental Design

The study was performed in a gutter system at the confluence of Ruisseau Boitel, the outlet of Lac Boitel, and the Rivière Mattawin, in the Réserve Saint-Maurice, Québec (46°57′N, 73°02′W). The gutter system, a multiple version of that described in Morin et al. (1988a), consisted of four large plastic sinks filled continuously by gravity with water from Ruisseau Boitel, and 12–16 sections (1.5 m long, 10 cm wide) of vinyl gutter fed from short pipes fixed to the drains of the sinks. Discharge from the sinks was controlled so that average current velocity was 0.4–0.5 $m \cdot s^{-1}$. Concentration of natural seston in the stream varied from 0.7 mg dry mass·L^{-1} at the lowest discharge of Ruisseau Boitel to 6 mg dry mass·L^{-1} during a major storm. We increased the range of seston concentrations in some experiments by supplementing the natural seston of Ruisseau Boitel with a mixture of powdered rabbit feed (particle diameter 10–250 μm) and kaolinite (particle diameter <2 μm). We filled Mariotte bottles, which empty at a constant rate, with a concentrated suspension of these particles, and connected the bottles to the pipes draining the sinks with a piece of Tygon tubing.

Bioassays were performed during May and June in 1986, concurrently to the ingestion experiments described in Morin et al. (1988b). Before each assay, several hundred larvae were collected from the outflow of Lac Boitel, from the outflow of neighboring lakes, or from the Rivière Mattawin, and transported live in buckets to the gutter system. Larvae were then transferred to the gutters, and left to acclimate for at least 6 h. Larvae were exposed to various concentrations (range 0.01–4.5 mg·L^{-1}) of Teknar HP-D, a commercial formulation of Bti, for 10 min, by delivering a concentrated solution of the formulation to the gutter by a Mariotte bottle. After 24 h, live and dead larvae remaining in the gutters were collected and preserved separately in 95% ethanol. Drift nets attached to the outlet of the gutters were used to collect any larvae that became unattached during the bioassay. Water temperature was measured during the application of Bti, and water samples were collected at the beginning, middle, and end of the Bti application. These water samples were filtered on preweighted 0.2 μm Nuclepore filters and seston dry mass was determined after drying the samples for 24 h at 60°C and cooling them in a desiccator.

Body lengths of preserved larvae were determined with a computerized image analysis system to assign larvae to 0.5-mm size classes, and the number of larvae that died or survived in each size class were recorded. Although larvae could be measured within a 0.05-mm precision, grouping of larvae into size classes was necessary to obtain more precision on the estimate of mortality rate.

Standard Assay Analysis

Simple linear regression is inappropriate to analyze dose–mortality responses because errors on percentages of mortality are not normally distributed, and because the variance of the estimates is a function of both the number of subjects tested and the expected percentage of mortality (Finney 1978). We therefore used maximum likelihood normit regression analysis to fit models of the form:

$$(1)\quad Z = a + b \log_{10} \text{Dose},$$

where Z is the normal deviate corresponding to the observed percentage of mortality (normit), a and b are fitted constants, and the dose (milligrams per litre times seconds) is the product of the concentration of Bti (milligrams per litre) and the contact time (seconds). Standardized residuals (Pearson residuals) to the fitted models were calculated by dividing the difference between the observed and predicted number of larval deaths by the standard error associated with the predicted number. Adequacy of the fit of the model to observed data was evaluated by the standard Chi-square test on the deviance (McCullagh and Nelder 1983) calculated as:

$$(2)\quad \text{Deviance} = 2\Sigma[R\ln(R/R') + (N-R)\ln((N-R)/(N-R'))]$$

where R and R' are the observed and predicted number of larvae killed, N is the number of larvae tested, and the summation is performed over all data points.

Improved Assay Analysis — Calculation of Specific Ingested Dose

The quantity of Bti ingested per unit mass (specific ingested dose, SID) was calculated as:

$$(3)\quad \text{SID} = \frac{IR \cdot DGUT \cdot t \cdot M\text{Bti}}{W \cdot (Q \cdot t \cdot [\text{seston}] + 0.2M\text{Bti})},$$

where IR is the volume of particles ingested by larvae per unit time (cubic millimetre per second), $DGUT$ is the density of the gut content of larvae (micrograms dry mass per cubic millimetre), t is the contact time (seconds), MBti is the mass of Bti used (milligrams wet mass), W is the dry mass of individual larva (milligrams), Q is the discharge (litres per second), [seston] is the concentration of natural seston (milligrams dry mass per litre) and the constant (0.2) is the conversion factor of wet mass to dry mass of the larvicide.

Ingestion rate, density of gut content, and dry mass of larvae were estimated from regression models:

$$(4)\quad \log_{10} IR = -6.55 + 2.36\log_{10} L + 0.034T - 0.63/[\text{seston}] + 0.61(\log_{10} L)/[\text{seston}] - 0.11D$$

$n = 4498 \quad R^2 = 0.86 \quad \text{RMS} = 0.055$
(Morin et al. 1988b)

(5) $\text{Log}_{10}DGUT = 3.28 - 1.42\text{Log}_{10}L$
$n = 44 \quad R^2 = 0.57 \quad \text{RMS} = 0.074$
(Morin et al. 1988a)

(6) $\text{Log}_{10}W = -2.68 + 2.93\text{Log}_{10}L$
$n = 53 \quad R^2 = 0.96 \quad \text{RMS} = 0.023$
(Morin et al. 1988a),

where L is the body length (millimetres, we used here the mid-point of the size class), T is the water temperature (°C), [seston] is the total seston concentration (including Bti particles, milligrams dry mass per litre), D is a dummy variable indicating the presence ($D = 1$) or absence ($D = 0$) of added particles of kaolinite and powered rabbit feed, n is the number of observations used to fit the model, R^2 is the coefficient of determination of the regression on transformed data, and RMS is the residual mean square of the regression.

Estimation and Evaluation of the Improved Model

Because of time constraints, and to maximize the amount of information per unit effort, only a subset of tested larvae were measured to estimate the specific ingested dose and fit the improved model (Table 1). Data for gutters in which less than 5% or more than 95% of the total number of larvae died were eliminated because such estimates have large sampling errors and correspondingly very little influence on the normit regressions. From the remaining data, we selected a subset to maximize the range of temperature, seston concentration, body length, and dose. The specific ingested dose of larvae of each size class in each gutter was then estimated by equation (3) using the mid-point of the size class as body length. The data were then fitted to a preliminary model of the form of equation (1) in which the specific ingested dose (micrograms Bti/milligram dry mass) replaced dose (milligrams per second per litre).

Adequacy of the resulting model could not be estimated by the standard Chi-square test because of the relatively large error on the independent variable (specific ingested dose), so a Monte Carlo simulation was used instead. Probabilities associated with the Chi-square test on the deviance around model of the form of equation (1) are asymptotically exact only if there is negligible error on the independent variable (McCullagh and Nelder 1983). Feeding rates of individual larvae varied from 30 to 300% of the mean predicted by equation (4) in the ingestion experiments performed concurrently (Morin et al. 1988b), and individual dry mass of larvae varied from 50 to 200% of the mean mass predicted by the length–mass regression (equation (6)); thus there was probably considerable variation around the estimate of specific ingested dose for larvae within a size class. Variability of the independent variable has the effect of reducing both the intercept and the slope of the normit regression. If the errors on the independent variable are normally distributed with a known variance (τ^2), the appropriate model to fit is (Hewlett and Plackett 1979):

(7) $Z = (\alpha + \beta X)/(1 + \beta^2\tau^2)^{0.5}$,

where X is the independent variable (Log specific ingested dose), α and β are the estimates of the "true" intercept and slope if there was no error on the independent variable, and τ^2 is the variance of the independent variable. Because the errors around the regression models (equations (4–6)) are approximately lognormally distributed and because the independent variable in equation (7) is the logarithm of the specific ingestion dose, it was possible to combine the estimates of variance around the regressions to obtain an estimate of τ^2. Estimates of α and β can be obtained by fitting equation (7) by maximum likelihood, or more directly by algebraic transformation from the observed estimates of intercept (a) and slope (b) from equation (1):

(8) $\beta = b/(1 - b^2\tau^2)^{0.5}$

(9) $\alpha = a(1 + \beta^2\tau^2)^{0.5}$.

Using these estimates of the "true" parameters, we obtained an empirical distribution of the deviance by Monte Carlo simulation. This allowed us to test the plausibility of the observed value considering the variability in individual specific ingested dose. A program was devised to go through the following steps: (1) for 500 iterations; (2) for each experiment; (3) for each size class represented in that experiment; (4) for each larvae in the

TABLE 1. Summary of assays. Water temperature (T, in °C), seston concentration (mg DM/L), dose (mg Bti·s^{-1}·L^{-1}), number of larvae (N), number of larvae that died (R). Asterisks and bold face denote data selected for the estimation of the model.

Assay	Gutter	T	[seston]	Dose	N	R
1	***9**	**15.8**	**1.4**	**6**	**215**	**39**
	***10**	**15.8**	**1.4**	**16**	**254**	**143**
	***11**	**15.8**	**1.4**	**40**	**1629**	**1353**
	12	15.8	1.4	2.6	1683	17
2	5	12	3.3	6	52	4
	***6**	**12**	**3.3**	**16**	**259**	**70**
	7	12	3.3	40	309	94
	***8**	**12**	**3.3**	**100**	**441**	**324**
	9	12	30.3	16	152	6
	10	12	30.3	40	162	13
	***11**	**12**	**30.3**	**100**	**511**	**143**
	***12**	**12**	**21**	**150**	**1420**	**684**
3	2	18.8	1.4	10	231	26
	6	18.8	7.7	63	846	90
4	***7**	**18**	**2.1**	**6**	**598**	**136**
	8	18	0.6	100	615	206
	9	18	2.1	250	628	558
	10	18	1.4	625	307	286
5	1	18	2.8	28	1086	27
	***2**	**18**	**2.5**	**173**	**744**	**581**
	3	18	3.8	28	732	35
	4	18	6	69	766	99
	***5**	**18**	**8.5**	**173**	**647**	**379**
	6	18	14.2	433	783	437
6	7	17.5	2.1	28	503	67
	8	17.5	2.1	173	640	360
	9	17.5	12.6	28	585	17
	10	17.5	12.6	69	548	60
	***11**	**17.5**	**24**	**173**	**492**	175
	12	17.5	7.8	433	462	421
7	***1**	**14**	**1.5**	**173**	**986**	**800**
	2	14	1.5	433	1170	1134
	3	14	1.5	1083	561	545
	***4**	**14**	**48**	**173**	**1271**	**105**
	***5**	**14**	**48**	**433**	**974**	**440**
	6	14	31	1083	920	870
	7	14	32	2707	394	363

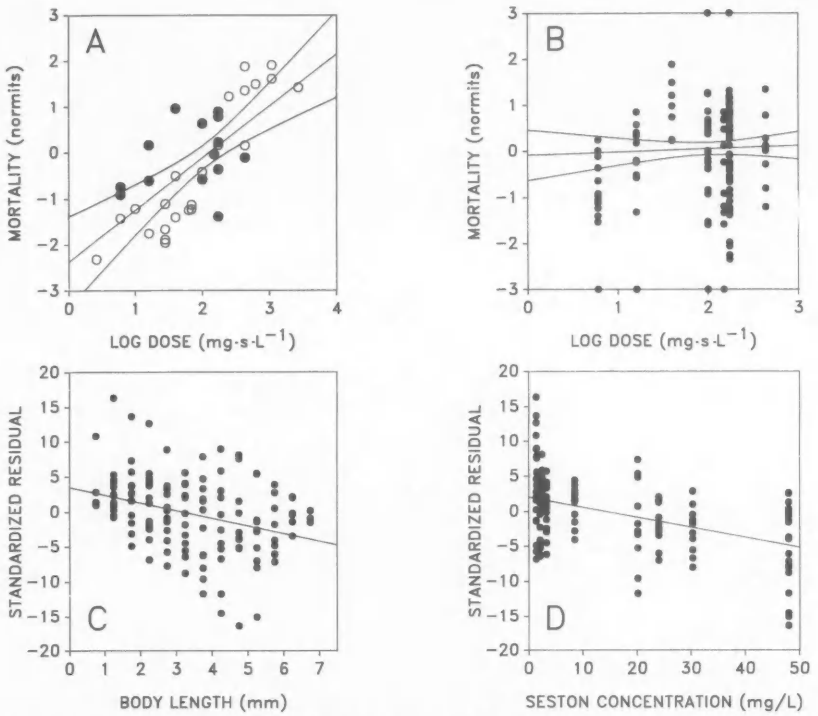

FIG. 1. Standard analysis. (A) Effect of dose on overall mortality in all experiments. Closed symbols are experiments selected for further analysis. Dotted lines are 95% confidence bands for mean mortality. Dose–mortality relation: $Z = -2.38 + 1.13$ Log dose, deviance = 7437, 35 *df* (B) Effect of dose on mortality in each size classes for the selected experiments ($Z = -0.09 + 0.07$ Log dose, deviance = 3839, 136 *df*). (C) Effect of body length on residual variability around model of Fig. 1b. (D) Effect of seston concentration on residual variability around model illustrated in (B).

size class (i) add measurement error on body length $U(-0.25$–0.25 mm), (ii) calculate Log *IR*, Log *DGUT*, Log *W* with error $N(0, \text{RMS})$ (equations (4–6)), (iii) calculate specific ingested dose for that larva (equation (3)), (iv) calculate probability (p) of response (equation (1) with α and β) (v) draw a random number (RND) $U(0$–$1)$ if RND$<p$ then larva dies, otherwise it survives; (5) Next larva (sum the number of deaths and get simulated mortality rate); (6) Next size class; (7) Next experiment (calculate normit regression (equation (1)) on simulated data using estimates of specific ingested dose from the real data set; store estimate of deviance); (8) Next iteration.

Where $U(x1$–$x2)$ denotes a uniform random number in the range $x1$–$x2$, and $N(0, \text{RMS})$ denotes a normal deviate with a mean of zero and variance equal to the residual mean square (RMS) of the regression model used. The probability of getting a deviance larger than the value observed for the real data set was then obtained by comparing the observed value with the cumulative distribution of simulated deviance values.

Finally we used an independent data set, composed of raw data on the percentage mortality of four species of simuliid exposed to various doses of a different formulation of Bti (Teknar WDC), to validate the improved model.

Results and Discussion

Standard Analysis

There was a weak relationship between dose and overall mortality (Fig. 1a). Although average mortality rate increased with the dose, the deviance value indicated that this model was inappropriate (Chi-square = 7437, 35 *df*, $p<0.0001$). Observed mortality of larvae that were measured and grouped by size class was almost independent of the dose (Fig. 1b), but negatively related to body length ($p<0.01$; Fig. 1c) and seston concentration ($p<0.001$; Fig. 1d).

Standard analysis of these results thus provided imprecise estimates of the effective dose, and moreover did not account for the systematic trend with body length and seston concentration. Although it may be argued that the large observed value of the deviance is not surprising given the heterogeneity of the larvae, and that better results may be obtained by considering size classes separately, the large scatter in Figs. 1a,b reflects the range of results that could be encountered in natural conditions. Besides, if the operational dose of larvicide were to be estimated from the average trend in Fig. 1a, control would be inadequate in streams with large larvae or high seston concentrations. Conversely, if most larvae are small and seston concentrations are low, the observed mortality will exceed what was planned, resulting in an unnecessarily high cost of control. A tighter relationship between desired and observed levels of control would therefore insure more replicable results, help keep the cost of control programs low, and minimize potential side effects of larvicidal applications.

Improved Model

Replacement of the standard dose by the specific ingested dose led to a much tighter dose–mortality relation (Fig. 2a).

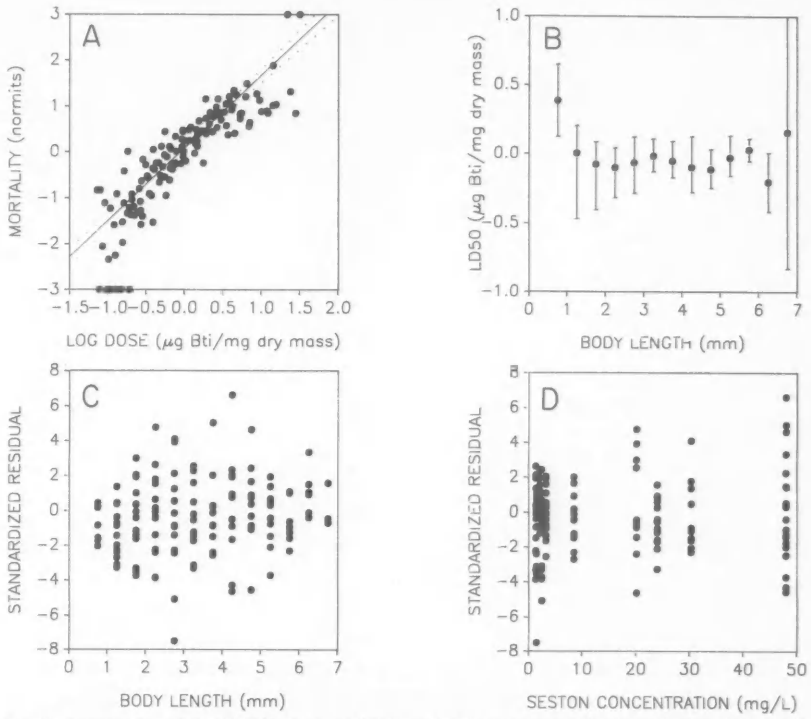

FIG. 2. Improved model. (A) Effect of specific ingested dose on mortality in each size class for the selected experiments ($Z = 0.08 + 1.58$ Log dose, deviance = 686, 136 *df*). (B) LD_{50} for each size class with 95% confidence intervals. (C) Effect of body length on residual variability. (D) Idem for seston.

TABLE 2. Specific ingested dose–mortality relations for individual size classes. Mid-point of the size-class (SC, in mm), intercept (*a*) and slope (*b*) of the regression relating the normit of mortality to the log of the specific ingested dose, and number of observations (*n*).

SC	*a*	*b*	*n*	Deviance
0.75	−0.91	2.36	7	2.8
1.25	−0.00	.53	14	47
1.75	0.12	1.55	14	79
2.25	0.16	1.51	14	82
2.75	0.08	1.13	14	80
3.25	0.02	1.33	12	29
3.75	0.10	1.75	12	50
4.25	0.19	1.83	11	95
4.75	0.21	1.84	11	45
5.25	0.06	1.81	11	34
5.75	−0.06	2.00	9	6
6.25	0.25	1.19	6	6
6.75	−0.11	0.70	3	0.8

When separate analyses were performed for each size class (Table 2), the LD_{50}'s were independent of size (Fig. 2b). This was further confirmed by analysis of the residual variability around the model (Fig. 2c). Seston concentration had no significant effect on residual variability (Fig. 2d).

The deviance around the improved model was much smaller than for the standard model but still much larger than the critical Chi-square value (deviance = 686, Chi-square = 164 for $\alpha = 0.05$ and 136 *df*). The simulation results showed that the observed deviance was still unlikely (approximate $p = 0.014$; Fig. 3) when the variability and error associated with the specific ingested dose of individuals were considered. However, most of the scatter around the fitted line could be attributed to imprecision of the estimate of specific ingested dose since the expected deviance around the fitted line was much higher (three to four-fold; Fig. 3) than what would have been expected if there was only negligible error on estimates of individual specific ingested dose. Nevertheless, the observed value of deviance is still unlikely, indicating that the improved model does

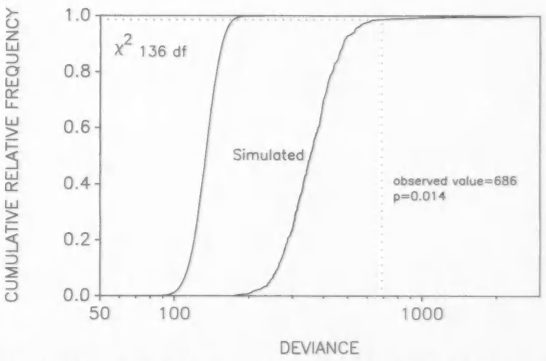

FIG. 3. Theoretical (Chi-square, 136 *df*) and simulated distribution of the deviance. Note that the expected deviance considering error in the independent variable (log specific ingested dose) is not distributed as chi-square, and that the simulation results indicates that the observed value of the deviance (dotted vertical line) is unlikely ($p = 0.014$).

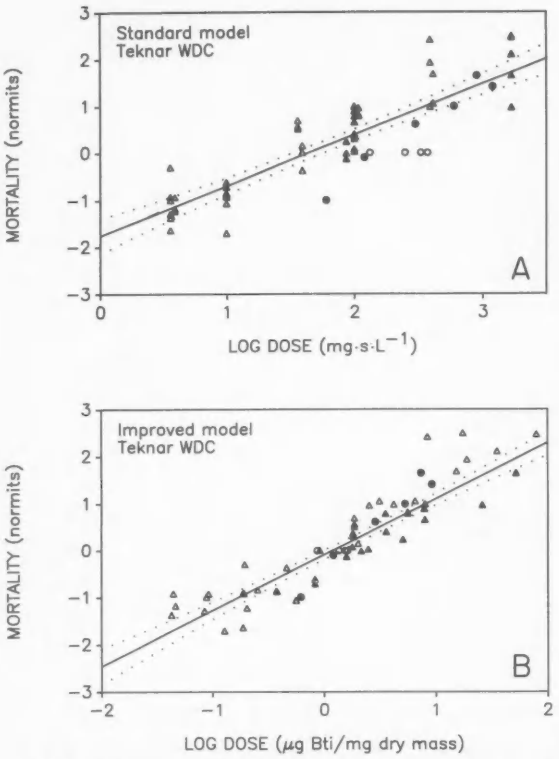

FIG. 4. Validation of the model. Normit regression analysis of assays of Teknar WDC by (A) the standard model ($Z = -1.77 + 1.08$ Log dose, deviance = 642, 61 *df*). (B) The improved model ($Z = -0.09 + 1.19$ Log specific ingested dose, deviance = 334, 61 *df*). Data from Colbo and O'Brien (1984) (Department of Biology, Memorial University St. John's, Nfld. A1B 3X9, unpubl. data; open circles, 4th instar of *Prosimulium mixtum/fuscum* at 5 and 10°C), Undeen et al. ((1984), closed circles, penultimate instar of *Simulium vittatum* at 22°C), C. Back (unpubl. data; open triangles, 1.5–5mm larvae of *Simulium venustum/verecundum* at 8–18°C), and C. Back (unpubl. data; closed triangles, 1.5–5mm larvae of *Simulium tuberosum* at 8–18°C).

not adequately fit the data, and suggesting that other factors besides the specific ingested dose influence mortality rate.

Significant lack of fit of normit or probit models in dose–response experiments is commonly attributed to the wrong choice of distribution for the tolerance (normal, logistic, Weibull, etc), to heterogeneity of the material tested (test animals differ in their intrinsic susceptibility for example when resistant and nonresistant strains are tested together), or to deficient experimentation (uneven distribution of the tested substance, errors in calculations or processing of the samples). All of these three common explanations may contribute to some of the apparently unexplained scatter around the predicted values. It is, however, unlikely that changing the assumed tolerance distribution would modify the statistical conclusion since the results of a similar simulation, where the normit model was replaced by a logistic model, lead to the same conclusion that the observed deviance was unlikely (approximate $p = 0.002$). Heterogeneity of the larvae or of the Bti formulation, and experimental deficiencies are more likely to contribute to the scatter around predicted values, although we cannot estimate the magnitude of such factors.

Alternatively, the significant lack of fit could be due to an incomplete or inappropriate model. Additional factors could be added to the model (for example particle size or gut passage time), or a different model could be constructed (for example considering that ingested Bti must be digested and transferred through the gut walls). We do not have the data to test such models, and additional research is needed to clarify these points.

We nevertheless accept the specific ingested dose model despite its imperfection because it is parsimonious and satisfactorily accounts for the effect of larval size and seston concentration. The model is parsimonious because it explains most of the apparent variability in susceptibility of larvae from only a subset of the factors affecting feeding rates (assumes no effect of particle size or type), and because it uses only parameters that are simple to measure (body length, total seston concentration, temperature). Moreover, the model accounts for the apparent positive relationship between lethal Bti dose and larval size, and decrease in Bti potency with increasing seston. The model therefore depicts adequately the effect of these two factors, although additional tests are required to more critically ascertain its validity with respect to temperature or contact time.

Validation of the Model

Use of the improved model leads to different conclusions concerning the toxicity of different batches of Bti or susceptibility of different species compared with what was concluded from the standard model. Standard analysis of bioassay results with Teknar WDC suggests that susceptibility among species varies, or that the potency of the various batches of formulation differs (Fig. 4a). However, when factors affecting the specific ingestion rate of formulation are taken into account by the improved model (Fig. 4b), the apparent discrepancies among species or tests are reduced and the overall deviance of the improved model (334) is significantly smaller than the deviance of the standard model (642) (Chi-square = 308, 1 *df*, $p < 0.0001$).

This validation suggests that the improved model is robust. Calculations of the specific ingested doses for the test data were made from rough estimates for two parameters: body length (from instar number, A. Morin, unpubl. data), and seston concentration (assumed 2mg/L for all tests). Moreover, it was assumed that the ingestion model of *S. venustum/verecundum* (equation (4)) holds for the other species outside the range of temperatures in which the model was originally estimated. Such an assumption casts doubt on the accuracy of our estimate of Teknar WDC potency, but this comparison indicates that specific ingested dose is a better correlate of observed mortality than the simple dose, and suggests that the improved model increases the replicability of results.

Practical Implications

The use of the specific ingested dose–mortality relationship is preferable to that of the standard dose–mortality relationship for testing various Bti formulations because it is not necessary to use larvae of fixed size or to control temperature or seston concentration. Because the model accounts for differences in susceptibility among larvae of different sizes, assays can be performed on larvae of various sizes without biasing the results, releasing one of the constraints on the supply of test animals. For assays performed in gutter systems, the improved model

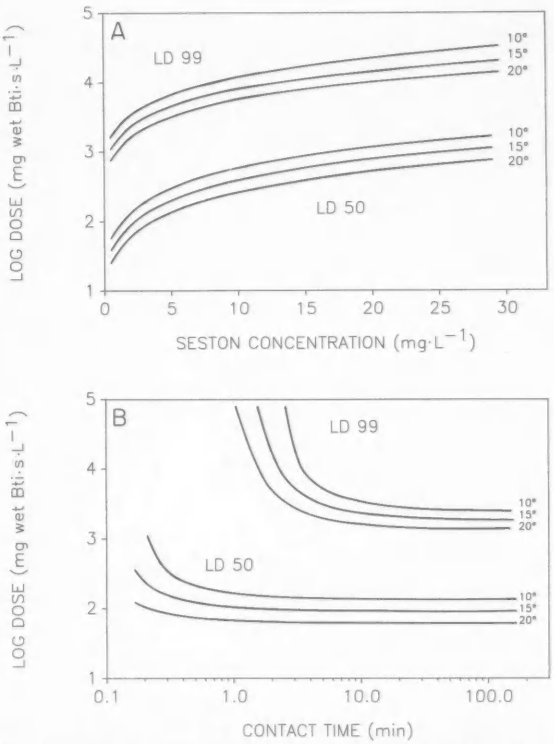

FIG. 5. Operational representation of the improved model. The lines are obtained by algebraic reformulation of the fitted equation (7) and replacing the specific ingested dose by its constituents (equation (3)). (A) Dose of Teknar HP-D required to kill 99 or 50% of last instars of *S. venustum/verecundum* (length = 6.5 mm) at various temperatures as a function of seston concentration. Solutions obtained for 10 min contact. (B) Effect of contact time on the dose required to kill 99 or 50% of last instar of *S. venustum/verecundum* (length = 6.5 mm) at various temperatures. Solutions obtained for a [seston] of 2 mg/L.

increases both the precision and the replicability of estimates of the LD_{50}, hence increasing the statistical power of comparisons among formulations.

For operational programs, an analysis of the model can indicate potential adjustments in treatments to insure adequate control in various conditions or to minimize the amount of formulation required. Because the specific ingestion rate of larvae declines with increasing size, the quantity of formulation required per unit discharge increases with larval size. Thus, treatments made early in the growing season may be advantageous. For instance, under average conditions in lake outlets ([seston] = 2 mg/L, temperature = 15°C, contact = 10 min), the LD_{99} of third instar larvae is only about 20% of that of last instar larvae. However, a single early treatment may be insufficient if larval recruitment is prolonged. In that case, two or three treatments at a reduced dose may be advantageous if the reduction in cost of the insecticide offsets the cost of multiple visits. Repeated treatments at low dosage may be particularly relevant in large rivers where the cost of insecticide is the highest.

Algebraic reexpression of equation (7) when specific ingested dose is expressed in terms of its constituents (equation (3)) allows us to calculate the amount of insecticide required in various situations. The amount of insecticide required per unit discharge decreases with increasing temperature, and increases with increasing seston concentration (Fig. 5a). The apparent increase in potency with temperature may be explained by increased feeding rates of larvae or increased digestion of Bti particles at high temperatures (Thompson 1987). Because there is commonly a large diurnal variation in the water temperature of lake outlets in early summer when most control programs are performed, treatment in late afternoons instead of early mornings will either reduce the amount of larvicide required, or increase mortality for the same price. The negative effect of seston concentration on apparent potency is attributable to a dilution of the formulation into the pool of particulates. The amount of larvicide formulation is almost a direct function of the product of the discharge and the seston concentration. Thus, significant reduction in cost could be achieved by restricting treatment to times when discharge and seston load are low.

Contact time can have a strong impact on the effective dose (Fig. 5b). Because the feeding rate of larvae eventually plateaus at high seston concentration, high mortality is impossible to achieve in very short contact periods because larvae do not ingest enough of the formulation. Minimum advisable contact times for 99% mortality incrase from about 5 min at 20°C to 10–15 min at 10°C. At low temperatures, the most efficient use of formulation is to release it over extended periods or to apply it upstream of the site to be treated and rely on the diffusion of the slug as it travels downstream to increase contact time.

Theoretical Implications

The feeding rates of larvae appears to explain most of the apparent variability in potency of the formulation tested. Hence, all factors contributing to an increase of the specific ingested dose will increase the level of control. However, the model also identifies individual variability in feeding rate as an important factor determining the mortality observed at a given dose. Unfortunately, few quantitative data exist on the variability of individual feeding rate in natural conditions. Estimates of such variability are required to make accurate predictions about the mortality rate in nature following larvicide application.

The effect of individual variability in feeding rate on observed mortality will be most important at extreme dosages. Examination of equation (7) reveals that the dose required to achieve 50% mortality is unaffected by the variability in feeding rate, whereas the LD_{99} would vary by almost two-fold if natural variability was 50 or 150% of estimated variance of specific ingested dose in the gutters. Thus, unless individual variability of specific ingested dose can be reproduced in assays, laboratory and even gutter tests will be inappropriate to determine accurately the LD_{95} or LD_{99} for operational treatments. Comparisons of the relative potency of various formulations should use the LD_{50} because it is the most precise, and theoretically the only level comparable with field estimates.

All factors increasing the variability of the specific ingested dose will also increase the dose required for effective control. Poor mixing of the formulation in the stream or habitat heterogeneity will add to the intrinsic variability of larvae and reduce observed mortality at high doses. Short contact times will also decrease observed mortality if larvae do not feed always at the same rate but pause periodically, for example to clean their head fans or reposition themselves. At extremely short contact times, all larvae not feeding at the instant of the passage of the insecticide will not be affected whatever the dose.

Conclusion

Ideally, control of black fly populations should be efficient, cheap, and without undesirable side effects. The proposed model predicts more accurately than older models the susceptibility of larvae to Bti formulations, and can be used to ascertain the efficacy of treatments, as well as to minimize the amount of formulation used, thus minimizing potential long-term impact. Combined with adequate descriptions of the carry of formulations in running waters, the model would allow improved optimization of large-scale control programs.

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Seasonal Development of Ice Algae and its Prediction from Environmental Factors near Resolute, N.W.T., Canada

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Welch, H. E., M. A. Bergmann. 1989. Seasonal development of ice algae and its prediction from environmental factors near Resolute, N.W.T., Canada. Can. J. Fish. Aquat. Sci. 46: 1793–1804.

Development of ice algae growing at the bottom of first-year congelation sea ice near Resolute, N.W.T. (75°N) was studied 1984–86. Ice algae moved downwards 1.5 cm·d^{-1} as the ice thickened. Biomass increased logarithmically with doubling times on the order of 4–8 d, reaching over 150 mg chlorophyll a ·m^{-2} in 1985 and over 300 mg·m^{-2} in 1986. Algal development was synchronous up to 120 km from the main study site. Snow cover controlled algal growth indirectly by its effect on light. Algal biomass was predictable from snow thickness and date, or snow thickness and light equally well (overall $r^2 = 0.77$ for 1985 and 1986 combined). Ice-associated amphipods were correlated with reduced ice algal biomass, but Si and NO_3 concentrations and tidal cycle had little or no detectable effect. Snow depth frequency distribution data are given. Peak ice algal biomass under low snow in 1986 was equal to 0.5 t dry weight and 4.7 kg Si ·ha^{-1}.

De 1984 à 1986, les auteurs ont étudié la croissance des algues des glaces qui se développent au bas de la glace de mer de première année forme par congélation près de Resolute, T. N.-O. (75° N). Les algues des glaces descendaient de 1,5 cm·d^{-1} à mesure que la glace s'épaississait. La biomasse a augmenté de façon logarithmique parallèlement aux temps de doublement de l'ordre de 4 à 8 d, atteignant plus de 150 mg Chl a·m^{-2} en 1985 et plus de 300 en 1986. Le développement des algues s'est fait de façon synchrone jusqu'à 120 km du principal endroit d'étude. La couche de neige a contrôlé indirectement la croissance des algues par son effet sur la lumière. On pouvait prédire la biomasse des algues d'après l'épaisseur de la neige et la date, ou encore d'après l'épaisseur de la neige et la lumière (r^2 de 0,77 pour les années 1985 et 1986 réunies). On a établi une corrélation entre les amphipodes associées aux glaces et une biomasse réduite d'algues des glaces, mais les concentrations de Si et de NO_3 ainsi que le cycle des marées a eu peu ou pas d'effet discernable. On fournit des données sur les distributions de fréquences de la hauteur de la neige. La biomasse maximale d'algues des glaces dans des conditions de faible enneigement équivalait à 0,5 t en poids sec et à 4,7 kg de Si·ha^{-1}.

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This research forms part of a larger project on quantification of the energy flow through the major components of marine mammal food chains in the Canadian arctic, focussing on the eastern Northwest Passage in the vicinity of Resolute, N.W.T. 74°42′N, 94°50′W (Fig. 1). It has been known for some time that the annual energy flow in the sea at Resolute is relatively high, some 120 g $O_2 \cdot m^{-2} \cdot yr^{-1}$ (Welch and Kalff 1974), and that ice algae blooming in late winter (March–May) contribute a significant fraction of total primary production (Welch and Kalff 1974). Microalgae, mostly diatoms, living amongst the small vertical crystals of freezing congelation sea ice, correspond to the "interstitial assemblage" of Horner et al. (1988), and are called simply "ice algae" herein. However, research on ice algae in the North American arctic indicates that the importance of ice algal production varies widely. Typical late May values for ice algal maxima are in the 7–25 mg chlorophyll *a* (chl) ·m^{-2} range (Apollonio 1965; Dunbar and Acreman 1980; Gosselin et al. 1986; Hsiao 1980; Horner and Schrader 1982). Alexander (1974) estimated annual ice algal production at Barrow, Alaska to be 5.0 g C·m^{-2}yr^{-1}. On the other hand, much higher figures are given by Smith et al. (1988) for Resolute, 77 to 225 mg chl·m^{-2} maximum standing crops and estimated annual net production rates ranging from 1 to 23 g C·m^{-2}·50 d^{-1} growing season, depending upon snow cover and year.

These figures suggest that the sea near Resolute does support above-average ice algal production. Comparisons between studies are made difficult, however, because of differences in sampling technique, lack of seasonal studies to provide a temporal framework for results, and few data on the environmental variables controlling production. The general applicability of results has also been hampered because studies have not been extended to areas other than the specific research site.

Accordingly, our goals in the present study were to describe the temporal cycle of ice algal biomass in Barrow Strait off Resolute, to model the biomass accumulation in terms of simple environmental parameters, and to verify those models as distant from Resolute as was logistically feasible.

Four environmental parameters, light, nutrients, substrate, and predation by grazers may be expected to influence ice algal growth rates. Light has been the environmental parameter most frequently cited as controlling ice algal growth, not surprising since the quantity of light reaching ice algae is typically 0.1 to 1% of surface light, and even less under high snow cover. Thus there is usually a negative relationship between snow depth and ice algal biomass during the exponential phase of the growing

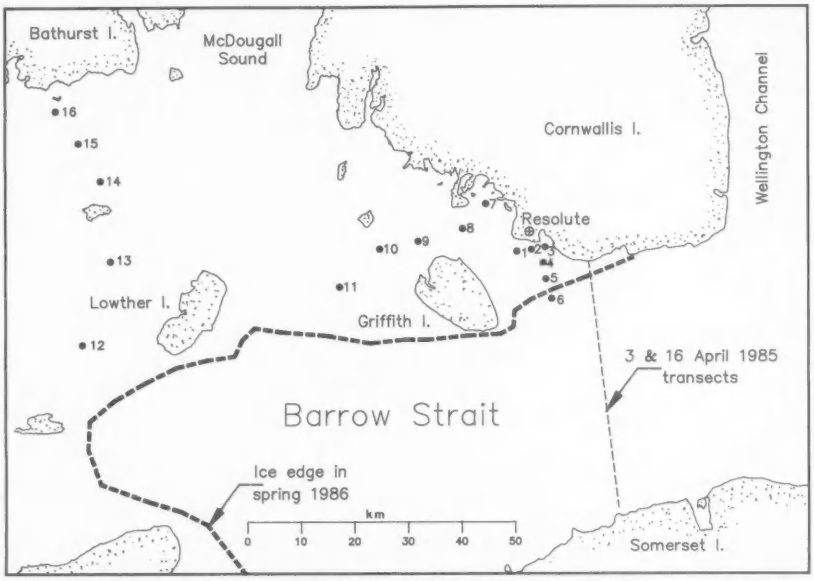

FIG. 1. Study sites near Resolute (74°43'N). Barrow Strait was completely frozen by March 1985 but remained partly open in 1986; the dashed line shows the western edge of the polynya. Sites 1–6 were routine sampling locations, as follows: (1) had low snow depth in 1985 and 1986; (2) had variable drifted snow cover in 1985 and 1986; (3) and (5) had low snow (1986 only); (4) had low snow (1985 only); (6) was thin new ice with low snow (1986 only); sites 7–10 were sampled on 15 April 1986; sites 11–16 were sampled 22 April 1986.

season (Gosselin et al. 1985, 1986; Horner 1985; Smith et al. 1988). Nutrient availability also influences ice algal growth, particularly in estuaries where stratification may limit the flux of nutrients. Thus ice algal growth is correlated with tidal currents near the Great Whale River (Gosselin et al. 1985), but the evidence for tidal cycles affecting growth via nutrient flux is weaker outside of estuaries (Cota et al. 1987). Two other factors that may limit ice algal abundance are substrate (the physical structure available for colonization) and various invertebrate grazers that are associated with ice algae (Carey and Boudrias 1987) and feed upon it (Lewis 1987), but we have found no data relating ice algal biomass to these two factors.

In the present paper we show how the seasonal development of ice algae at Resolute is a function of overlying snow cover and light, discuss the influences of other environmental variables, demonstrate that the results are applicable up to 120 km from the main study area, and place the results in the context of other arctic ice algal studies.

Site Description

Most work was done within a few kilometres of Resolute in Barrow Strait, with comparative distributional studies conducted up to 120 km from Resolute (Fig. 1). Maximum water depth within 25 km of Resolute is about 120 m, with water depths >200 m both to the west (Viscount Melville Sound) and east (eastern Barrow Strait) (Fig. 1). Fast ice in Barrow Strait breaks up in July. Freeze-up begins in the bays in September and extends over most offshore areas north and west of Resolute by late October, resulting in a nearly-continuous sheet of first-year congelation ice with occasional patches of trapped multi-year ice. Barrow Strait is a high-energy area, with a dominant west to east current (Prinsenberg and Bennett 1987), an occasional small westerly counter current along the north shore (H. E. Welch, unpubl. data), and diurnal tides up to 2 m, such that current velocities typically range from slack to >60 $cm \cdot s^{-1}$ near Resolute (Cota et al. 1987; T. Siferd, Freshwater Institute, Winnipeg, Man., pers. comm.). The ice between Cornwallis and Somerset islands (Fig. 1) does not consolidate until late winter; in some years the Lancaster Sound shorelead, an extension of the North Water polynya, extends as far west as Griffith Island, within 10 km of Resolute (Smith and Rigby 1981). In 1985 that area froze about 5 March, resulting in flat young ice between Resolute and Somerset. In 1986 consolidation did not occur and the freezing ice-edge (Fig. 1) enabled us to sample ice algae in new, rapidly-freezing ice.

Snow falls primarily in spring and fall, usually during storms, and accumulates as wind-blown drifted snow pack. Although newly-fallen and drifted snow is relatively soft and may be eroded subsequently by wind, the processes of sintering, sublimation, and consolidation of drifts usually results in stable drifts which subsequently change very little until melt (H. E. Welch, unpubl. data). Thus snow depth may increase at a particular point, but it rarely decreases. Areas with very low snow cover remain, ranging from ≈1 m^2 to many square kilometres depending upon location, data, and ice surface topography. The surface of these "low snow" areas appears like stucco, being composed of old hoarfrost sometimes overlain by 1–2 cm of snow.

Methods

Laboratory Procedures

We used the quantity of chl *a* extracted from the ice algal community as our measure of ice algal abundance (Bunt and

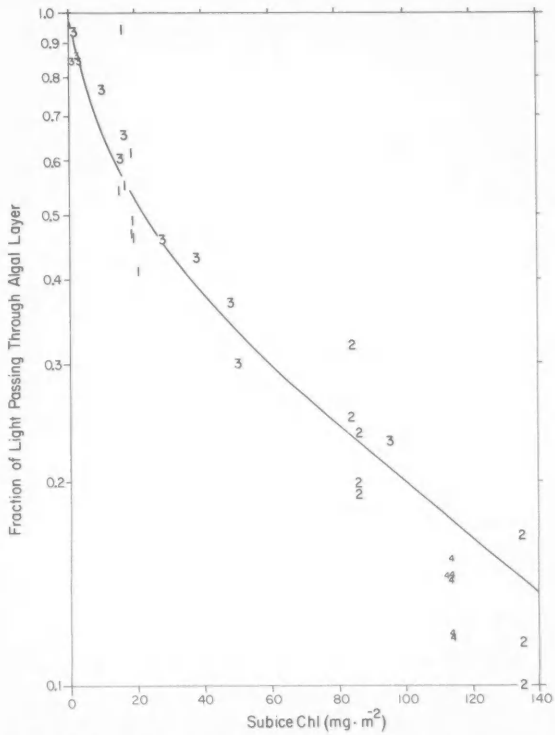

FIG. 2. Calibration curve for the light scraper, showing the fraction of light absorbed by the algal layer (light reading before scraping) divided by (light reading after scraping) as a function of subice chlorophyll measured from core samples. Curve is $Y = 1.102 - 0.196 \ln \text{chl}$; $n = 38$, $r^2 = 0.90$. Straight line extrapolation used for chl ≤ 4 mg·m^{-2}. (1) = SIPRE cores and diver cores (Welch et al. 1988), 22 April 1985 site 1. (2) = SIPRE cores 1 May 1986, sites 1, 4 and 6. (3) = SIPRE cores and diver cores, 2 May 1985, site 2. (4) = SIPRE cores and diver cores, 14 May 1985, site 4.

Lee 1979). Field samples were kept dark and cold. In the laboratory they were melted and filtered through Whatman GF/C filters before passive extraction in 95% methanol and reading in a Turner model III fluorometer calibrated against lettuce chl annually. Details of this procedure and the calculation of chl per square metre are given in Welch et al. (1988).

Reactive Si, NO_3, and soluble reactive P were analyzed according to Stainton et al. (1977) using a Technicon autoanalyzer and specifications (1977 version). Biogenic Si was converted to reactive Si by boiling algal samples for 1 h in 0.1 M NaOH and neutralizing with HCl (Lewis 1987).

Algal dry weight:chl ratios and Si:chl ratios were determined on ice algae suctioned by diver on 8 May 1985 and 3 and 19 May 1986. Algae were concentrated by settling in a darkened glass Imhoff cone and small amounts pipetted onto tared polycarbonate filters. Filters were dried at 60°C, reweighed, and then analyzed for biogenic Si. Chlorophyll concentrations were determined from known volumes of the same algal suspension (see Lewis 1987 for details).

Field Procedures

Snow measurements

Snow depth frequency distributions were measured at four sites, each judged to have a uniform drift pattern and mean

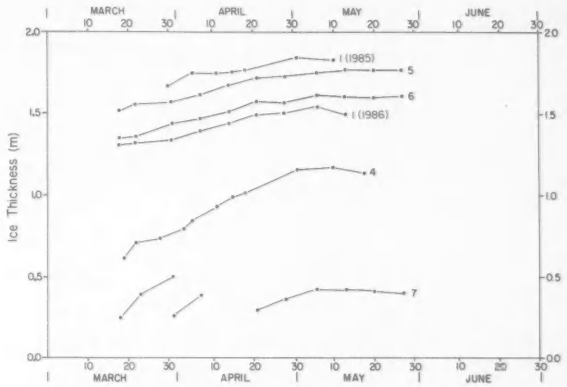

FIG. 3. Ice thickness as a function of time at various sites in 1985 and 1986.

snow depth. Observers walked toward an object on the horizon, taking snow depths to the nearest centimetre with a meter stick, at 5-m intervals. After 250–500 m the observer walked perpendicular to the line 20 m, repeated the procedure back to a point near the starting place, did the same to the other side of the starting place, then drove forward 5–30 s on a snowmobile and repeated the procedure.

Measurement of subice algal biomass

Early in the year the subice community was sampled using a standard 7.3-cm inside diameter SIPRE corer. Later in the season when the ice ceased freezing and the ice algae began to slough from the ice surface, we used two alternate methods to measure algal abundance. The "light scraper", used in 1985, consisted of a Licor 185 2π sensor in a toothed holder on the end of a buoyant under-ice arm, and was based on the principle that algal biomass should be inversely proportional to light transmission through the algal layer. Light readings were made below the algal layer, the layer was then scraped away to a depth of 2.5 cm, and readings made again. Absorbance by the algal layer was calibrated against SIPRE cores and cores taken by diver (Fig. 2). To measure sub-ice algae in 1986 we used the subice suction corer (SSC), a remotely-operated drill and suction device which excavated a 6-cm diameter × 2.5 cm deep hole and brought the material to the surface. SIPRE cores underestimated late-season ice algal chl by as much as 90% compared with SSC estimates. Details of the above procedures are given in Welch et al. (1988).

Our routine sampling scheme consisted of two sets of weekly samples. The first was on relatively large (10^2 to 10^4 m^2) areas of low snow (see above, "stucco") (sites 1, 3–6 in Fig. 1). We expected to find maximum algal development at these low snow sites.

The second sample set was at site 2 (Fig. 1), a uniform area of drifted snow ranging from 3 to 50 cm depth. We expected data from this variable-snow site to define relationships between algal biomass and snow depth. At all sampling sites we measured ice thickness in the sampling hole and snow depth directly above the chl sampling site, to the nearest centimetre.

We calculated the mean abundance of algal chl for each site with varying snow cover as:

$$(1) \quad \sum_{n=0}^{n=k} F_n \text{Chl}_n,$$

where F_n = proportion of the area at snow depth n, Chl_n = chl (milligrams per square metre) at each snow depth n (from regressions in Table 2) and k = maximum snow thickness (centimetres).

If the chl:snow equation predicted higher chl at low snow depths, we used an upper limit equal to the maximum chl found at the low-snow sites on that date, to avoid erroneously high calculated mean chl for a given mean snow depth.

Other measurements

To investigate the effects of ice-associated amphipods on ice algal biomass, we took chl samples adjacent to holes used for sweep-net samples of amphipods (Pike and Welch 1989).

Weekly water column samples for nutrient analyses were taken about 5 km offshore beyond site 2 (Fig. 1), over 110-m water depth.

Results

Distribution of Algae in the Ice

For 12 SIPRE cores taken on low-snow sites between 7 April and 6 May 1986, 88.9% of the chl in the bottom 10 cm was in the 0–2 cm layer and 7.3% was in the 2–4 cm layer, for a mean of 96.3 ± 7.4% (95% CI) in the bottom 4 cm. We therefore assume that our routine SIPRE coring, where the bottommost 4 cm was sampled, accounted for practically all the subice algal layer. The SSC only sampled to a depth of 2.5 cm, but even so, SSC and SIPRE core samples were no different early in the season, and later the SSC samples were higher (Welch et al. 1988). The light scraper also sampled to a depth of 2.5 cm, but was calibrated against SIPRE cores (Fig. 2). We are therefore confident that estimates of ice algal chl are reasonably accurate.

The ice algae remained concentrated in the bottom 2 cm even though ice thickness increased at some sampling sites by at least 1.5 $cm \cdot d^{-1}$ (Fig. 3). The ice algae must therefore have been mobile, moving downward with the growing ice crystals at the same average rate, a minimum of 1.5 $cm \cdot d^{-1}$. We have seen no reference made to this mobility of the ice algal community.

Algal Development at Low-Snow Sites

Ice algal chl increased log-linearly March–May at all but one low-snow site (Fig. 4). Doubling times calculated from the regressions ranged from 3.7 to 7.4 d (Table 1). The fastest doubling times were for the youngest and thinnest ice, 4.1 d for ice ≈0.4 m thick and 3.7 d for ice ≈1 m thick, both at site 6. The low-snow site (3) that behaved differently (Fig. 4) began in March 1986 with similar chl and a doubling time of 6.3 d for the first 3 wk. Chlorophyll accumulation then ceased abruptly, peaking at only 40 $mg \cdot m^{-2}$ on 20 May compared with >300 $mg \cdot m^{-2}$ at site 5.

In 1985, peak chl occurred by 10 May at ≈175 $mg \cdot m^{-2}$ (Fig. 4) and it did not begin to decline until 16–18 May at site 4, and not until after late May at site 6. In 1986 chl continued to increase log-linearly to 325 $mg \cdot m^{-2}$ on 20 May, then dropped rapidly four to six-fold by the following week (Fig. 4). Low snow sites were not monitored after May in either year because subice algae began to slough off (diver observations), and because algal chl was continually monitored at the variable-snow site (below).

Once ice algae were established and began to grow under uniform low-snow conditions, slight differences in chlorophyll per square metre between sites, corresponding to only a few days growth, were maintained through time. This "head start" phenomenon is shown by Fig. 5, where differences between four sites were maintained during the period of most active growth. These differences were correlated with the thickness (age) of the ice and probably resulted from the relative age of the established algal communities.

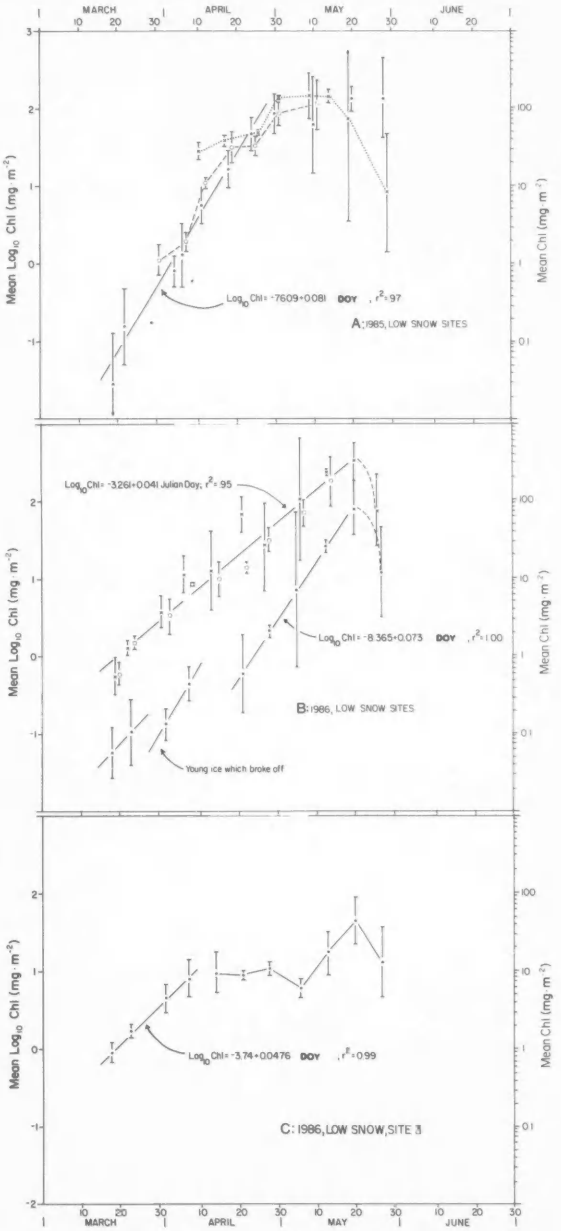
MARCH
APRIL
MAY
JUNE
Mean Log10 Chl (mg·m-2)
Mean Chl (mg·m-2)
Log10 Chl = -.7609+.0081 DOY , r2=.97
A; 1985, LOW SNOW SITES
Log10 Chl = -3.261+.041 Julian Day, r2=.95
Log10 Chl = -8.365+.073 DOY , r2=.100
B: 1986, LOW SNOW SITES
Young ice which broke off
Log10 Chl = -3.74+.0476 DOY , r2=.99
C: 1986, LOW SNOW, SITE 3

FIG. 4. Chlorophyll development at low-snow sites, means ±95% CI (includes both sampling and analysis variance). See Fig. 2 for ice thickness data, Fig. 1 for locations. Some points offset by 1 d for clarity. A (1985): ○ = site 1; × = site 4; ● = site 6. B (1986): ○ = site 1; × = site 5; ● = site 6. C (1986): ● = site 3.

TABLE 1. Doubling times for subice algal chlorophyll at Resolute, calculated from regressions in Fig. 4 and data in Fig. 14.

Site	Inclusive dates (day/month/year)	No. of days	Doublings per day	Doubling time, (d)	r^2	N
6	18/3–30/4/1985	44	0.21	3.7	0.97	9
6	21/4–20/5/1986	31	0.18	4.1	1.00	5
1 + 5	18/3–20/5/1986	59	0.10	7.4	0.95	19
3	18/3– 7/4/1986	20	0.12	6.3	0.99	4
4.8 cm $\bar{x}$ snow	26/3–17/5/1986	52	0.12	6.1	0.96	7
10.1 cm $\bar{x}$ snow	26/3–17/5/1986	52	0.09	8.1	0.94	7
21.4 cm $\bar{x}$ snow	26/3–17/5/1986	52	0.11	6.4	0.95	7

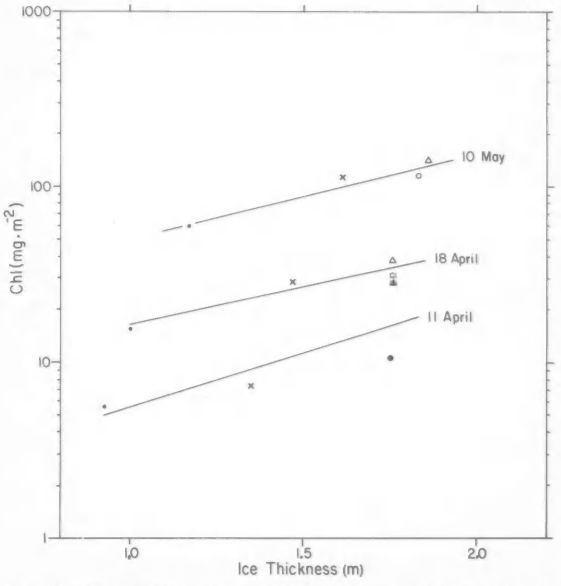

FIG. 5. Chlorophyll development at four low-snow sites as a function of ice thickness on three sampling days in 1985. ● = site 6, × = near site 5; ○ = site 1; Δ = site 4.

Algal Development Beneath Variable Snow Cover, Site 2

Algae began to grow first where snow depth was least. In both years the March and early April data were closely approximated by log chl:log snow depth relationships (e.g. Fig. 6a), whereas by mid-April a log-linear fit became best (Fig. 6b). Snow depth was thus a good predictor of chl, with an overall mean r^2 of 0.75 ($n = 9$) for 1985 and a mean r^2 of 0.79 ($n = 12$) for 1986. The chl:snow depth regressions are summarized in Table 2.

Algal biomass remained a negative function of snow depth until the algae began to slough beneath areas of low-snow cover. For example on 25 June 1986, chl beneath >11 cm snow was still a negative function of snow depth, whereas beneath <11 cm snow it was a possitive function of snow depth (Fig. 6c).

The single set of chl:snow depth observations made in 1987 fit closely with the 1985 and 1986 data (Table 2). The chl calculated from the regression for 2–3 cm of snow on 8 May 1987 was 120–135 $mg \cdot m^{-2}$, the same as was found on 8 May 1985 and 1986 for the low snow sites (Fig. 4). From these results we conclude that ice algal development is highly synchronous at Resolute from year to year.

Ice Algal Development distant from Resolute

The western edge of the polynya froze abruptly in early March 1985, leaving a remarkably uniform, smooth, snow-free ice sheet extending 55 km across Barrow Strait from Cornwallis to Somerset Island. Twice, on 3 and 16 April, we sampled nine stations equidistant on a transect between the two islands (Fig. 1), three SIPRE cores per station. On 3 April the ice was 0.7 m thick (site 6, Fig. 3) and chl ranged between 0.32 and 0.90 $mg \cdot m^{-2}$. On 16 April the ice was 1.0 m thick and chl ranged from 3.5 to 6 $mg \cdot m^{-2}$ at the nine stations. Since the doubling time of algae on this ice sheet was under 4 d (Table 1, site 6), the development of algal biomass must have been highly synchronous and uniform across the entire ice sheet.

On 15 April 1986 we took 10 SIPRE cores each at sites 7–10, 12 to 35 km west of Resolute (Fig. 1). The results fit well with those from the routine variable-snow sampling site 2 taken the next day (Fig. 7), with chl averaging slightly higher under low snow to the west. The western samples probably had higher chl at each snow depth because they were taken beneath slightly thicker ice than those at site 2, demonstrating the "head start" phenomenon beneath older ice noted earlier (Fig. 5).

On 22 April 1986 we made an extensive survey 50 to 120 km west of Resolute (Fig. 1), sampling only low snow (1.5–3.5 cm) and 10-cm snow depths. The results (Fig. 8) were of the same magnitude as those obtained the following day at site 2, but were more variable. Two phenomena explained some of this variability. First, a storm on 10–11 April had left newly-drifted snow, and samples from points overlain by new snow (detectable by texture) had higher than expected chl (Δ's in Fig. 8) as a result of residual algae produced when the snow depth had been less. Second, the subice surface at two low snow sites was eroded and the algae partially sloughed (x's in Fig. 8), because the weather on 20–22 April was clear and relatively mild (−17 to −20°C; Fig. 9), with low wind speeds (14, 10, and 7 $km \cdot h^{-1}$, respectively).

From these three sets of results, we conclude that ice algae within 120 km of Resolute grow in synchrony, having similar biomass beneath similar ice and snow cover for the same times.

Termination of the Bloom by Melting

Because the algal layer absorbs so much of the radiation that reaches it (over 90% at high biomass levels; Fig. 2), there may be active melting of the skeletal layer and consequent sloughing of algae while air temperatures are still well below freezing, if solar radiation is high. In 1985 sloughing occurred on 30 April after 6 d of clear skies, despite air temperatures of −23° to −15°C (Fig. 9). The early and relatively low chl asymptote in 1985 (Fig. 4) probably resulted from relatively early ice sub-

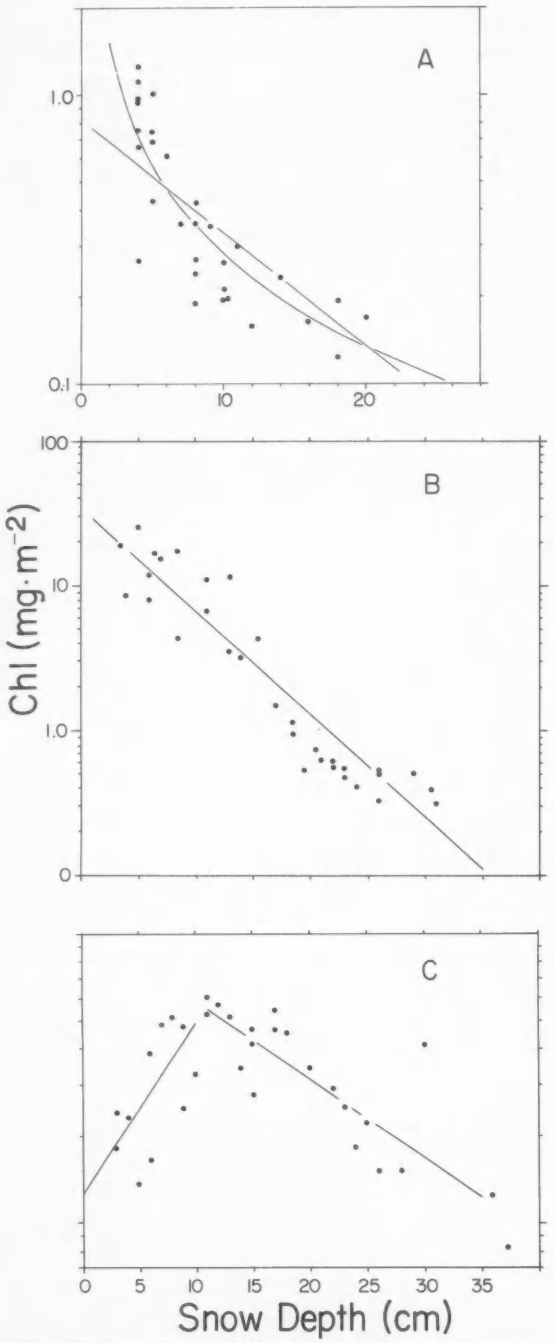

FIG. 6. Subice chlorophyll distribution as a function of overlying snow depth at site 2. (A) 26 March 1986. Linear fit is $\log_{10}\text{chl} = -0.0884 - 0.0389$ snow, $r^2 = 0.56$, $n = 32$; curve is $\log_{10}\text{chl} = 0.4917 - 1.047 \log_{10}\text{snow}$, $r^2 = 0.73$, $n = 32$. (B) 30 April 1986; (C) 25 June 1986; see Table 2 for regression coefficients.

strate changes caused by continuous above-normal temperatures (Fig. 9) and clear skies (not shown).

In contrast, a brief warm spell (−3.3°C) in early May 1986 (Fig. 9) was not accompanied by clear skies, and air temperatures subsequently dropped back to −10 to −12°C through 27 May; as a result the algae did not slough. However, a succession of clear days 23 to 27 May 1986 (Fig. 9) was enough to melt the skeletal layer and slough the algae, reducing chl by several fold the week ending 27 May (Fig. 4). Higher snow sites retained algae until after 19 June 1986, when warm temperatures (Fig. 9), and high irradiance abruptly terminated the bloom under all snow conditions (Fig. 5).

Correlation between Ice-Associated Amphipods and Chl

Simultaneous sampling for chl and ice-associated amphipods on transects near Resolute in 1986 showed a negative correlation between chl and amphipod biomass, but the correlation was poor ($r^2 = 0.21$; Fig. 10). There was a better correlation between water depth and chl ($r^2 = 0.71$; not shown). At site 3, where water depth was only 20 m and chl peaked at only 40 $\text{mg}\cdot\text{m}^{-2}$ (Fig. 4), divers reported fairly high densities of amphipods, several 10's per square metre. Site 3 also served as a routine collecting site for the ice amphipods *Weyprechtia pinguis* and *Onisimus glacialis* (Lewis 1987).

Nutrients

Soluble reactive P averaged 1–2 $\mu\text{g}\cdot\text{L}^{-1}$ throughout the water column. Although P tended to be slightly higher below ≈25 m depth, there was no trend with time and no evidence of depletion by ice algae.

Dissolved nitrate was always stratified, with sharp increases occurring in the 25–40 m depth range, paralleling the distributions of Si (below). Typical values were 2–5 $\mu\text{g}\cdot\text{L}^{-1}$ immediately beneath the ice and 10–15 $\mu\text{g}\cdot\text{L}^{-1}$ N at 75 and 100 m depths. Despite the strong vertical stratification, regressions of water column nitrate summed over various depths (e.g. 2–5 m, 2–30 m, etc.) versus time gave nonsignificant slopes, indicating little correlation between nitrate and ice algal growth. However, NO_3 concentrations were highly variable week to week, and obviously reflected the movement of different water masses through the sampling site.

Silicon also showed vertical stratification, with increases coming about 20–30 m depth (Fig. 11). Regressions of water column total Si (2–100 m) against time gave nonzero slopes ($P < 0.05$), equal to 278 $\text{mg}\cdot\text{m}^{-2}$ for March–June of 1985 and 1986 (data not shown). Water column totals for 0–30 m or less showed no significant trends. As with NO_3, Si concentrations were highly variable (Fig. 11) and probably reflected the movement of various water masses past the sampling site.

Conversion Factors

From data collected 5 May 1985, and 3 and 19 May 1986, we found an ice algal dry weight:chl factor of 137:1 ± 58.5 (95% CI; $n = 20$), and a Si:chl ratio of 13.0:1 ± 4.2 ($n = 12$).

We also use a C:chl ratio of 37:1 (Cota et al. 1987 for Resolute ice algae; Bunt and Lee 1972 for antarctic ice algae).

Discussion

Control of Ice Algal Growth by Environmental Factors

Four factors can be expected to control ice algal growth: substrate, grazers, nutrients, and light, each discussed in turn below.

TABLE 2. Relation between subice chlorophyll and snow depth at site No. 2, for snow depths ≤30 cm Light = light scraper; SSC = subice suction corer; N = number of field samples; LL = Log_{10}chl = $a + (b)$ (log_{10} snow depth); SL = Log_{10}chl = $a + (b)$ (snow depth).

Date	Sampling method	N	Best fit model	r^2	a	b
30 March 1985	SIPRE	21	LL	0.50	1.73	−2.27
5 April	SIPRE	23	LL	0.77	2.29	−2.46
12 April	SIPRE	31	LL	0.81	5.13	−4.24
22 April	SIPRE	30	SL	0.60	1.88	−0.066
26 April	SIPRE	27	SL	0.59	2.18	−0.067
2 May	SIPRE, Light	61	SL	0.80	2.25	−0.077
10 May	Light	15	SL	0.83	3.27	−0.125
20 May	Light	13	SL	0.94	3.13	−0.097
28 May	Light	27	SL	0.88	3.34	−0.096
26 March 1986	SIPRE	31	LL	0.73	0.49	−1.05
2 April	SIPRE	30	LL	0.70	0.89	−1.37
16 april	SIPRE	30	LL	0.70	1.06	−1.11
23 April	SIPRE	31	SL	0.62	1.44	−0.059
30 April	SIPRE	30	SL	0.89	1.59	−0.076
8 May	SIPRE, SSC	44	SL	0.91	2.39	−0.087
17 May	SSC	22	SL	0.90	2.63	−0.062
22 May	SSC	29	SL	0.88	2.64	−0.053
28 May	SSC	29	SL	0.89	2.74	−0.063
3 June	SSC	26	SL	0.87	2.59	−0.056
10 June	SSC	32	SL	0.62	2.34	−0.043
19 June	SSC	29	SL	0.77	2.54	−0.034
25 June[a]	SSC	19	SL	0.55	2.00	−0.024
25 June[b]	SSC	11	SL	0.32	1.16	+0.046
8 May 1987	SIPRE	34	SL	0.65	2.24	−0.054

[a]At snow depth <11 cm.
[b]At snow depth ≥11 cm.

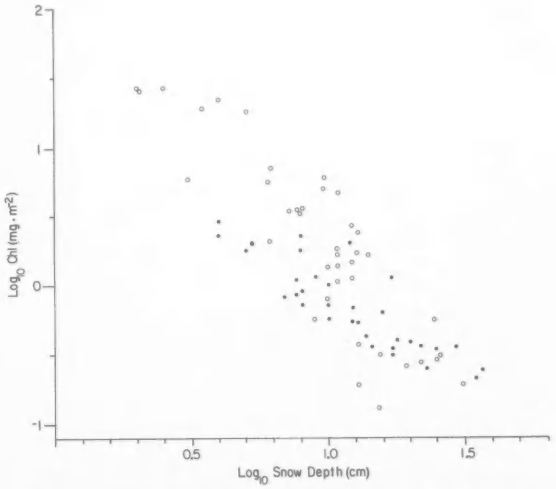

FIG. 7. Subice chlorophyll distribution as a function of overlying snow depth at site 2 (●) on 16 April 1986, and sites 7–10 (○), 12 to 35 km west of Resolute on 15 April 1986. Regression coefficients for site 2 are given in Table 2.

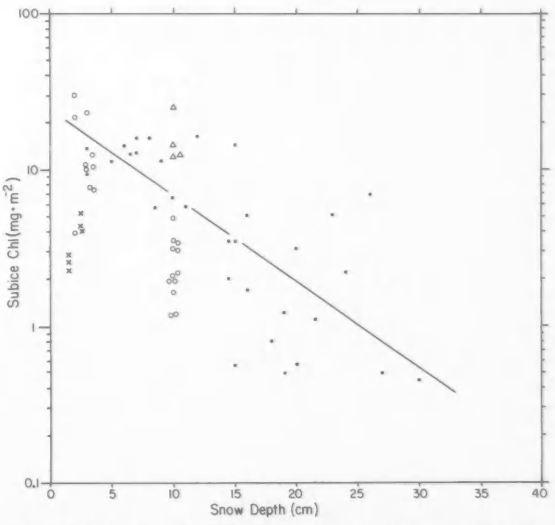

FIG. 8. Subice chlorophyll distribution as a function of overlying snow depth at sites 50 to 120 km west of Resolute on 22 April 1986, compared with results from regular sampling site 2 the next day. ○ = remote samples; × = remote samples with visible degradation of the skeletal ice layer; Δ = remote samples overlain by variable quantities of newly-drifted snow; ● = regular samples from site 2 on 23 April, where log_{10} chl = 1.44 − 0.059 snow, $n = 31$, $r^2 = 0.62$.

Substrate

Substrate (space to live) limits growth in that the approach of summer results in the melting of the skeletal layer and the sloughing of algae at its peak development. We assume that earlier in the spring, when both ice and algae are actively growing, substrate is not limiting at Resolute. However, in estuaries

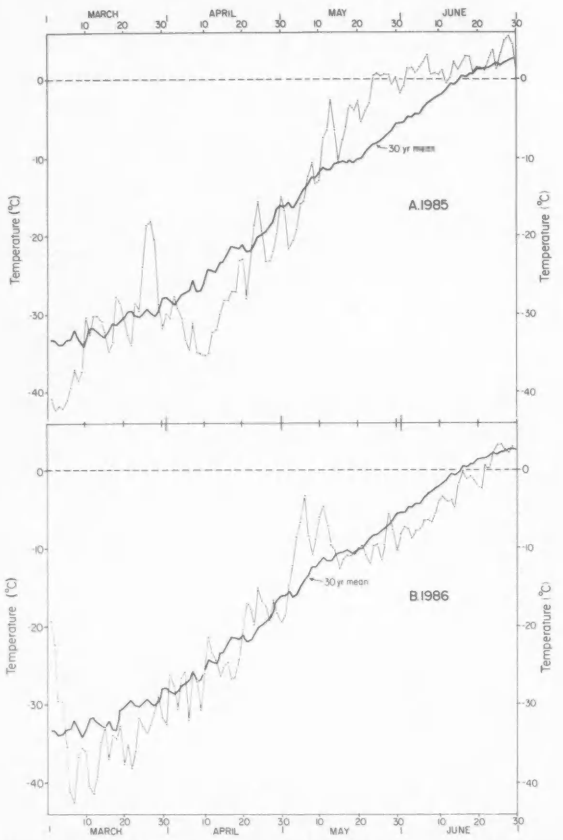

FIG. 9. Mean daily air temperature March–June at Resolute, from Environment Canada records.

where ice forms from low-salinity water, substrate does apparently limit algal growth (Gosselin et al. 1986). Note also that ice algae cannot grow in normal freshwater ice either, because of the smooth solid nature of the underice surface.

Grazers

Ice-associated amphipods were negatively associated with ice algal biomass over shallow water (Fig. 10), and were probably the cause of the low algal peak at site 3 in 1986. Divers saw virtually no amphipods at other sampling sites, where water depths were >75 m, so it is unlikely that amphipods affected ice algal biomass at any site other than site 3. Conover et al. (1986) reported that the copepod *Pseudocalanus minutus* forms dense aggregations beneath the ice at Resolute (at times so dense as to reduce horizontal visibility; H. E. Welch, unpubl. data), and guts are full of ice algae, but they were unsure whether *Pseudocalanus* were removing algae from the ice or simply grazing sloughed cells in the water column.

It appears that while grazers do reduce ice algal abundance in shallow water, they have no detectable effect over deep offshore waters of Barrow Strait.

Nutrients

The great week to week variability of NO_3 (not shown) and Si concentrations (Fig. 11) hindered interpretation. The

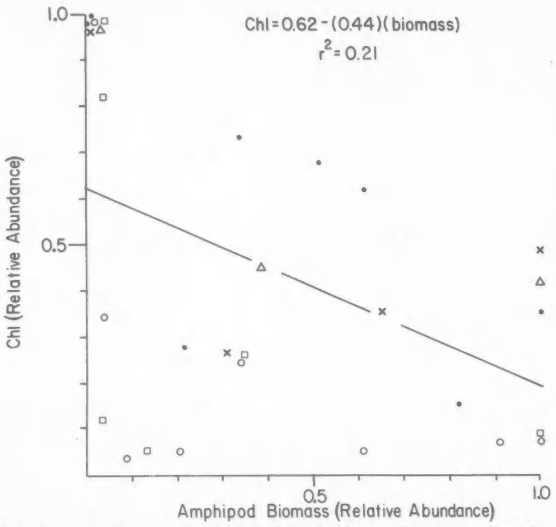

FIG. 10. Abundance of subice chlorophyll as a function of subice amphipod biomass on transects near Resolute (see Fig. 1 for locations). ● = 10 May 1986 site 1; ○ = 14 May 1986, 5 km east of sites 3–4; × and Δ = 2 May 1987, two transects on the east side of Griffish Island; □ = 14 May 1987 site 2. $Y = 0.62 - 0.44\,x$; $r^2 = 0.21$, $n = 29$. For each transect, relative abundance was calculated by dividing each value by the maximum value, to facilitate comparison across times and locations.

decrease of Si in the 2–100 m water column from March to June 1985 and 1986 was 278 mg·m^{-2}, the equivalent of 21.4 mg chl·m^{-2}. This is much lower than our estimate of mean algal mass in the Resolute area (see discussion below). There was weak stratification in the 20–40 m depth range (unpubl. CTD profiles; see also Prinsenberg and Bennett 1987), so changes in Si and NO_3 below that depth may not even have been caused by ice algae; yet water column integrations from 2–30 m gave nonsignificant slopes for Si and NO_3 in both years. If nutrients were exerting much control over algal growth we should have found biomass changes correlated with spring and tidal cycles (Cota et al. 1985; Gosselin et al. 1985), which we did not. The addition of Si and NO_3 concentrations to a model of ice algal growth (discussed below) improved the model r^2 by less than 0.02. Thus we find little evidence that Si or NO_3 concentrations were limiting the growth rate of Resolute ice algae.

Light

We were unable to obtain unbiased measures of light reaching the ice algal community because the vertical distribution of algae (and therefore light absorption) inside the ice varied with time, resulting in great week to week variability for light readings taken inside holes drilled upwards into the ice to a constant depth of 2.5 cm. Had we been able to take light readings from deeper in the ice, say 10–15 cm upward, there would have been less residual chl and better consistency between dates and locations.

Nevertheless, our data show that light is the primary factor regulating ice algal development at Resolute.

Under relatively constant ice thickness, light to the algal layer is controlled by snow depth (extinction coefficient $\approx 0.22 \cdot cm^{-1}$, compared with $\approx 1.0 \cdot m^{-1}$ for sea ice), resulting

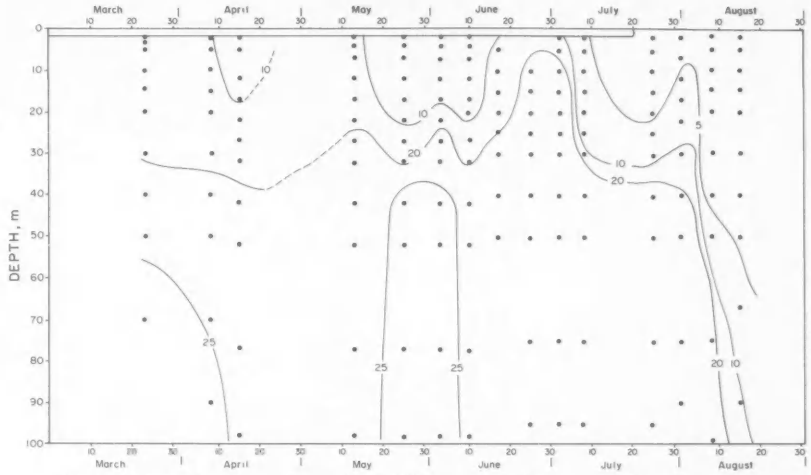

FIG. 11. Isopleths of Si concentration (milligrams per cubic metre) at Resolute, 1985.

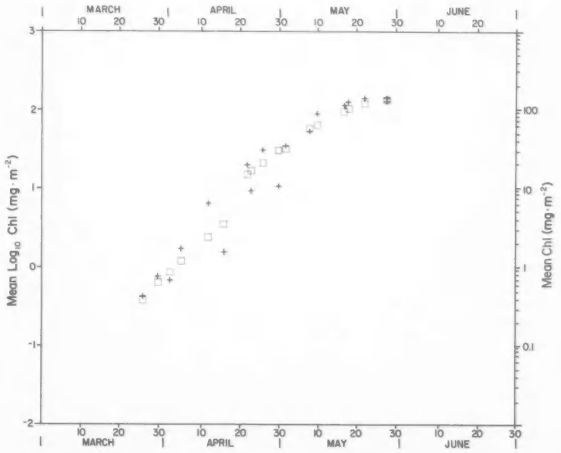

FIG. 12. Mean chl per square metre calculated for a 10.0 cm mean snow depth (frequency distribution in Fig. 14), comparison between 1985 and 1986 data and a generalized model output. + = 1985 and 1986 combined, calculated from equations of chl × snow depth in Table 2; □ = 1985 and 1986 combined equations (2) and (4) predicting chl (*f*) snow depth and time, Table 3.

in consistently high correlations between chl and snow (Fig. 6; Table 2). Chlorophyll should therefore be predictable from just two variables, snow depth and cumulative light. Using a $\log_{10}$ transformation of cumulative light to the top of the snow in millieinsteins per square metre per day (incoming solar radiation to the RF-1 field, Environment Canada records for Resolute, megajoules energy per square metre per day times 45.7) and the chl:snow data for each sampling date (same data as used in Table 2), we do find high correlation coefficients, averaging 0.76, for chl predicted from snow and light (Table 3). Both snow and light explain equal amounts of the model variation (mean $r^2 = 0.39$ and 0.37, respectively).

Because light first returns to Resolute about 5 February, and because cumulative light from February to May tends to be very similar year to year, it is possible to substitute time for light in our model with no loss of predictive power. Using a modified Day of the year (DOY) calendar starting with 5 February as day 1, we found that the variable ($\log_{10}$ cumulative day) had the same predictive power as $\log_{10}$ cumulative light (Table 3). The model can therefore be used to predict algal biomass beneath first-year sea ice as a function of date and snow depth, or light and snow depth, with a reasonable degree of accuracy over the time period March to early June.

An example is given in Fig. 12, where mean algal chl is calculated from day and snow depth (equations (2) and (4) in Table 3) for a mean snow cover of 10.1 cm (depth frequency distribution in Fig. 13), and compared with outputs for each date according to the primary snow:chl relations in Table 2. Although there is an obvious break between the log/log and semi-log portions of the predicted values, the model corresponds to our belief that surface light and snow depth are major factors controlling ice algal development at Resolute. The addition of Si and NO_3 concentrations immediately below the ice to the model improved the r^2 by an average of <0.02.

Annual Maximum Ice Algal Biomass near Resolute

In 1985 there were thousands of square kilometres of smooth ice with <3 cm snow cover resulting from delayed freezing of the polynya between Cornwallis and Somerset islands (Fig. 1). This habitat, represented by site 6 in Fig. 1, developed 140 mg chl·m^{-2} (Table 4). However, most sea ice is snow-covered to some extent; the problem is that there are no data on wide area snow depth frequency distributions anywhere in the arctic. But we are able to combine our chl:snow equations (Table 2; Fig. 4) with snow depth frequency distributions for three representative areas (Fig. 14) to estimate mean chl under those specific snow conditions for 1985 and 1986 (Fig. 14). Maximum algal biomass development for various sites is given in Table 4, along with dry weight, C and Si equivalents. The maximum biomass recorded, 360 mg chl·m^{-2}, equalled 0.5 t dry matter and 4.7 kg Si·ha^{-1}.

Based on our knowledge of snow and ice cover, we suggest that a reasonable annual maximum standing crop in Barrow Strait is 100 mg chl·m^{-2}, the equivalent of 13.7 g dry matter, 1.3 g Si, and 3.7 C·m^{-2}. Interestingly, Smith et al. (1988) calculated annual ice algal production to have been 3.3 g C·m^{-2}

TABLE 3. Least-squares correlation coefficients (r^2) for variables in the equation $Y = a + bX_1 CX_2$, where $Y = \log_{10}$chl (milligrams per square metre), X_1 = snow depth (centimetres), and X_2 = either $\log_{10}$ cumulative surface light or $\log_{10}$ cumulative DO4, where day 1 = 5 Feb (in brackets). Chlorophyll and snow data used to caculate the equations are the same as those used to calculate the regressions in Table 2, where $\log_{10}$ chl:$\log_{10}$ snow fit best before 16 April and $\log_{10}$ chl:snow fit best after 16 April.

Time period	n	Equations	Log_{10} snow	Log_{10} light	(Log_{10} day)	ϵr^2	(ϵr^2)
1985, 30 Mar.–12 Apr.	75		0.32	0.47	0.48	0.79	0.80
1986, 26 Mar.–16 Apr.	91		0.39	0.39	0.39	0.77	0.78
Combined, 26 Mar.–16 Apr.	166	[a]+[b]	0.23	0.38	0.36	0.61	0.59
Time period	**n**	**Equations**	**Snow**	**Log_{10} light**	**(Log_{10} day)**	**ϵr^2**	**(ϵr^2)**
1985, 22 Apr.–28 May	173		0.54	0.23	0.23	0.77	0.77
1986, 23 Apr.–2 June	185		0.41	0.45	0.46	0.86	0.87
Combined, 22 Apr.–3 June	358	[c]+[d]	0.46	0.32	0.32	0.78	0.78
	Mean		0.39	0.37	0.37	0.76	0.76

[a] $\text{Log}_{10}\text{chl} = -8.631 - 1.580 \log_{10}$ snow $+ 1.956 \log_{10}$ cumulative light.
[b] $\text{Log}_{10}\text{chl} = -8.951 - 1.522 \log_{10}$ snow $= 5.746 \log_{10}$ cumulative day.
[c] $\text{Log}_{10}\text{chl} = -14.01 - 0.0708$ snow $+ 2.898 \log_{10}$ cumulative light.
[d] $\text{Log}_{10}\text{chl} = -11.57 - 0.0698$ snow $+ 7.040 \log_{10}$ cumulative day.

TABLE 4. Maximum biomass of ice algae near Resolute. Conversion factors: dry weight:chl for Resolute ice algae = 137 (SD = 28.0; $n = 20$; data from 5 May 1985, 3 and 19 May 1986); Si:chl = 13.0 (SD = 1.9; $n = 12$; same dates as above); C:chl = 37 (Cota et al. 1987 for Resolute ice algae; Bunt and Lee 1972).

Date	Location	Ice (m)	Snow (cm)	Chl ($\text{mg}\cdot\text{m}^{-2}$)	Chl ($\text{g dry wt}\cdot\text{m}^{-2}$)	($\text{g}\cdot\text{m}^{-2}$)	Si ($\text{g}\cdot\text{m}^{-2}$)
28 May 1985	Site 6	1.5	< 3	140	19	5.2	1.8
28 May 1985	South of Cape Martyr	1.8	$\bar{x} = 4.8$	112	15	4.1	1.5
28 May 1985	Wellington Channel	—	$\bar{x} = 10.1$	125	17	4.6	1.6
28 May 1985	Site 2	1.7	$\bar{x} = 21.4$	44[a]	6	1.6	0.6
20 May 1986	Site 5	1.6	< 3	360	50	13.3	4.7
20 May 1986	Site 6	0.4	< 3	80	11	3.0	1.0
28 May 1986	South of Cape Martyr	1.5	$\bar{x} = 4.8$	288	40	10.7	3.7
19 June 1986	Wellington Channel	—	$\bar{x} = 10.1$	178	24	6.6	2.3
19 June 1986	Site 2	1.5	$\bar{x} = 21.4$	78	11	2.9	1.0

[a] Probably was higher after 28 May; see Fig. 15.

beneath 8–12 cm of snow in 1985 at Resolute, based on a maximum standing crop of 2.5 g $\text{C}\cdot\text{m}^{-2}$. Although synoptic prediction of ice algal production must await better data on snow depth distribution, it is clear that ice algae comprise a significant fraction of total energy flow, estimated to be 48 g $\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in Resolute Bay itself (Welch and Kalff 1975).

Comparison with Other Studies

Smith et al. (1988) also worked on ice algae at Resolute in 1985–86 and found chl values up to 225 $\text{mg}\cdot\text{m}^{-2}$, close to our peak values of >300 $\text{mg}\cdot\text{m}^{-2}$ in late May 1986 (Fig. 4). Smith et al. may not have been able to sample maximum biomass with SIPRE cores, because we found that our own SIPRE cores underestimated ice algal biomass at the time of maximum development (Welch et al. 1988). The peak biomass Smith et al. and we found at Resolute is much higher than has been found elsewhere in the Canadian arctic (e.g. Apollonio (1965) for Jones Sound; Dunbar and Acreman (1980) for Robeson Channel, Viscount Melville Sound, and Hudson Bay at Churchill; Gosselin et al. (1986) for southeast Hudson Bay; Hsiao (1980) for Frobisher Bay). However, comparisons with the above-mentioned studies are difficult to make because of potential underestimates using SIPRE cores and the probable effects of differential grazing, currents, nutrient concentrations, snow and ice thickness, and time of year. No study to date has examined all these variables simultaneously.

Several other studies have found evidence that ice algal production is light limited (Smith et al. 1988; Gosselin et al. 1986; Grossi et al. 1987 in antarctic waters). Nutrient availability, particularly NO_3, has also been implicated by correlations between bursts of growth and spring tides (Gosselin et al. 1985; Maestrini et al. 1986; Cota et al. 1987). The extensive work done in Manitounuk Sound (Gosselin et al. 1985, 1986) documented the response of ice algae to estuarine conditions, but because the waters were brackish and strongly stratified, and peak chl levels were low (typically 10–30 $\text{mg}\cdot\text{m}^{-2}$), caution must be used when extrapolating to the full sea water conditions found elsewhere.

Conclusion

It is gratifying that ice algae in Barrow Strait can be predicted from date and snow thickness. Knowledge of snow distribution and photosynthetic parameters (e.g. Smith et al. 1988), will enable wide-area estimates of ice algal production to be made for the first time. As knowledge of ice algal dynamics expands, so will our knowledge of other factors controlling ice algal development. Ideally future studies should simultaneously consider light, nutrients, grazing pressure, and substrate, across a gradient of conditions. This will require the development of new techniques (for example, to measure substrate), and cooperative efforts amongst several researchers because of the great

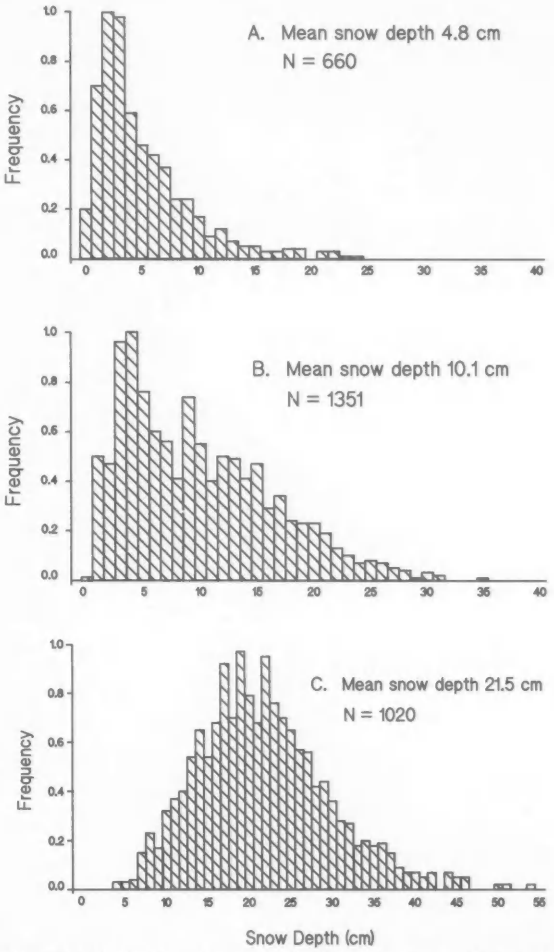

FIG. 13. Distribution of snow depth frequencies, normalized to the modal frequency, at three sites. A = site 1, 23 May 1986. B = West side of Wellington Channel, between Barlow Inlet and Helen Haven, 26 April 1986. C = Site 2, 20 May 1986.

difficulty in collecting large amounts of data simultaneously under arctic conditions. Until we have synoptic ice algal production data, knowledge of Arctic marine ecosystem dynamics will remain incomplete.

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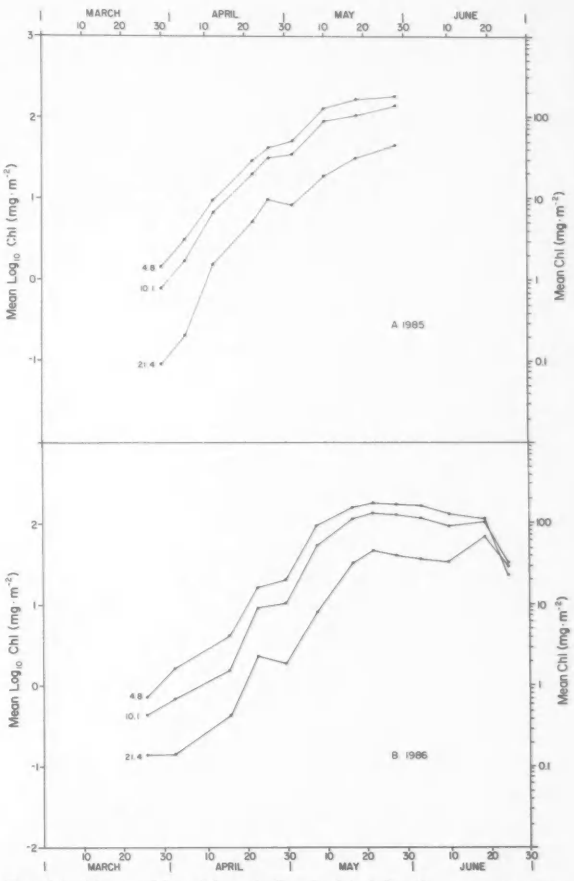

FIG. 14. Mean subice chlorophyll calculated for three mean snow depths. A = 1985; B = 1986.

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Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns

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Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. Aquat. Sci. 46: 1805–1818.

Long-term discharge records (17–81 yr) of 78 streams from across the continental United States were analyzed to develop a general quantitative characterization of streamflow variability and predictability. Based on (1) overall flow variability, (2) flood regime patterns, and (3) extent of intermittency, 11 summary statistics were derived from the entire record for each stream. Using a nonhierarchical clustering technique, nine stream types were identified: harsh intermittent, intermittent flashy, intermittent runoff, perennial flashy, perennial runoff, snowmelt, snow + rain, winter rain, and mesic groundwater. Stream groups separated primarily on combined measures of intermittency, flood frequency, flood predictability, and overall flow predictability, and they showed reasonable geographic affiliation. A conceptual model that incorporates the nine stream clusters in a hierarchical structure is presented. Also, the positions of the 78 streams in a continuous three-dimensional flow space illustrate the wide range of ecologically important hydrologic variability that can constrain ecological and evolutionary processes in streams. Long-term daily streamflow records are a rich source of information with which to evaluate temporal and spatial patterns of lotic environments across many physiographic and ecographic regions. Relative positions of streams in flow space provide a conceptual framework for evaluating a priori the relative importance of abiotic and biotic factors in regulating population and community processes and patterns.

On a analysé des données recueillies chaque jour pendant des périodes prolongées (de 17 à 81 ans) sur 78 cours d'eau du territoire continental des États-Unis en vue d'établir une caractérisation quantitative générale de la variabilité et de la prévisibilité de l'écoulement. On s'est servi de la variabilité générale de l'écoulement, des caractéristiques du régime des crues et du degré d'intermittence pour tirer 11 types de statistiques sommaires de l'ensemble des données recueillies sur chaque cours d'eau. Au moyen d'un technique de groupage non hiérarchique, on a défini neuf types de cours d'eau : courant fort, intermittent, crue éclair, intermittent, ruissellement intermittent, crue éclair, permanent, ruissellement permanent, fonte des neiges, neige et pluie, pluie hivernale et eaux souterraines, conditions moyennes. Essentiellement, on a regroupé les cours d'eau d'après un ensemble de mesures de l'intermittence, de la fréquence et de la prévisibilité des crues et de l'écoulement général, et l'on a constaté une association raisonnable au point de vue géographique. On présente un modèle conceptuel où les neuf groupes sont organisés suivant une structure hiérarchique. Par la position qu'occupent les 78 cours d'eau étudiés dans l'espace d'écoulement tridimensionnel, on peut voir qu'il y a une grande variabilité hydrologique d'importance écologique et que cette variabilité peut restreindre les processus écologiques et évolutionnaires dans les cours d'eau. Les registres quotidiens constitués à long terme sur l'écoulement sont une source d'information précieuse pour l'évaluation de l'environnement lotique en fonction du temps et du lieu dans un grand nombre de régions géomorphologiques et écologiques. La position relative des cours d'eau dans l'espace d'écoulement constitue un cadre conceptuel qui permet d'évaluer a priori l'importance relative des facteurs abiotiques et biotiques dans la régulation des processus et de l'organisation des populations et de la communauté.

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Importance of environmental variability as a factor structuring biological communities has been of long standing interest to ecologists (Hutchinson 1961; Slobodkin and Sanders 1969; Menge and Sutherland 1976, 1987; Wiens 1977, 1984; Connell 1978; Sousa 1984; Pickett and White 1985; Chesson 1986). The extent of variability is often viewed as regulating the relative contributions to community structure of abiotic and biotic processes (e.g. Menge 1976; Menge and Sutherland 1976, 1987; Peckarsky 1983; Wiens 1984) and can serve as an a priori criterion for predicting community pattern and process (Wiens 1984). Stream ecologists are interested in this theory because of the great temporal variability within and between lotic environments, particularly with respect to streamflow. Flow, arguably the most characteristic physical attribute of stream ecosystems, plays a central role in stream ecology (see Hynes 1970). Because streamflow exerts control over many important structural attributes in streams (e.g. habitat volume, current velocity, channel geomorphology, and substratum stability), flow measures represent an integration of complex environmental conditions.

Much recent debate has centered around placing stream communities along some conceptual axis (e.g. equilibrial to nonequilibrial (Wiens 1984)) that corresponds to a physical environmental gradient, often streamflow (e.g. Grossman et al. 1982; Peckarsky 1983; Minshall and Petersen 1985; Reice 1985; Lake and Barmuta 1986; Moyle and Vondracek 1985; Ross et al. 1985, 1987; Angermeier 1987; Heins and Matthews 1987; Matthews 1987; Schlosser 1987; Minshall 1988; Power et al.

1988; Resh et al. 1988). A quantitative description of the variability and temporal predictability of discharge conditions for a set of widely distributed (in space) streams would provide a context for delineating the range of physical environmental variability under which ecological and evolutionary processes operate in lotic habitats. The physical environment could thus be viewed more objectively and a priori predictions of community structure formulated. Such a spatial and temporal perspective of natural environmental variability is lacking not only in stream ecology (Peckarsky 1983; cf. Ward 1989) but in other systems as well (e.g. see Halfpenny and Clark 1988).

In streams, flow fluctuations and extreme conditions such as floods and low or zero flow are primary sources of environmental variability and disturbance, respectively (cf. Stanford and Ward 1983). Patterns of diversity of all major lotic assemblages, including fish (Seegrist and Gard 1972; Harrell 1978; Horwitz 1978; Minckley and Meffe 1987), invertebrates (Vannote et al. 1980; Ward and Stanford 1983; Bournard et al. 1987), attached algae (Patrick 1975; Peterson 1987; Power and Stewart 1987), and macrophytes (Haslam 1978; Ladle and Bass 1981) have been related to patterns of temporal variation in flow. Moreover, there is a substantial body of evidence indicating that both high flow (flood) and low flow (intermittency) disturbances play a central role in structuring stream communities (Hynes 1970; Williams and Hynes 1976, 1977; Iversen et al. 1978; Fisher 1983; Stanford and Ward 1983; Ward and Stanford 1983; Schlosser 1987; Delucchi 1988; Minshall 1988; Power et al. 1988; Resh et al. 1988).

Different combinations of streamflow variation (e.g. range and predictability), patterns of flooding (e.g. frequency and predictability), and extent of intermittency result in different degrees of physical control over biotic organization. Yet, of the limited number of comparative geographical studies, few have considered several mesures of flow variability simultaneously. Consideration of mean flow conditions (Hawkes et al. 1986; Moss et al. 1987; Townsend et al. 1987), variation about the mean flow (Horwitz 1978), and short-term estimates of flood frequency (Cushing et al. 1980, 1983; Minckley and Meffe 1987; Fisher and Grimm 1988) have been used, but only M. Gurtz (in Resh et al. 1988) and Bunn et al. (1986) have incorporated formal measures of temporal predictability (using monthly data) into an analysis. No previous work has used long-term mean daily discharge data to compare flow variability, along with its temporal components, across many spatially-dispersed streams. Given daily data, it is also possible to characterize the temporal components of the disturbance regime, i.e. frequency, timing, and duration of floods and intermittent conditions. Disturbances here are defined according to Sousa (1984, p. 356) as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established." Floodplain communities (sensu Welcomme 1979) will not be considered.

The objectives of this paper are to (1) develop an objective and general quantitative characterization of streamflow variability and predictability using long-term mean daily discharge records, (2) analyze flow reords for 78 streams across the continental United States to provide a framework for evaluating the relative variability of any particular stream's physical flow environment, (3) assess hydrologic similarity between streams using components of the flow regime that are of probable ecological significance, and (4) use the results, in conjunction with ecological theory and the limited available empirical data, to suggest possible relationships between hydrologic pattern and population and community level processes and patterns in streams.

Methods

Selection of Streams

The 78 streams chosen for this study (Fig. 1) represented most of the major stream geomorphologic (Brussock et al. 1985), physiographic (Fenneman 1946), and ecographic (Baily 1980; Omernik 1987) regions of the continental United States. Gauged stations were selected from the USGS Water Resources Survey Papers and the entire periods of record (17 to 81 yr) of average daily flow values for all 78 sites were acquired on magnetic tape. We assumed the available records were an unbiased representation of the various streams' flow histories. An attempt was made to include only streams with minimal perturbation (based on the summaries in the Water Survey Papers). For example, excluded streams were those that were impounded or had impounded upstream tributaries, that were channelized, that had more than minimal upstream diversion for irrigation or water supply, or that were similarly impacted. Given the broad geographic distribution of the streams investigated, we used mean annual discharge per unit watershed area, rather than stream order or mean discharge, as an indicator of stream and watershed size (Hughes and Omernik 1983). Summary data for these streams are included in the Appendix.

Derivation of Variables

Daily mean flow values for all stations were read from magnetic tape and analyzed using FORTRAN 5 programs and statistical software packages (MINITAB, BMDP, SPSSX) on a Control Data Corporation CYBER 840 computer. All flow values were transformed by a natural logarithm function ($\ln [x+1]$) so streamflow frequency distributions would approximate a log-normal distribution (see Markovic 1965). Each set of transformed data was then "modularized" by dividing each daily flow value by the grand mean for the period of record (i.e. modularized mean flow = 1.0) for that stream to produce a dimensionless flow index that facilitates comparison between streams (Yevjevich 1972).

Four variables describing stream setting were included in the analysis. Basin area (AREA), mean annual flow (ANNQ), and a size scalar, mean annual flow divided by basin area (Q/AREA), were provided by the Water Survey summaries. The fourth, LNANNQ, was taken as the grand mean flow of the ln-transformed data. These variables are defined in Table 1 and their numerical values for each stream are given in the Appendix.

Three general categories of derived statistics to describe the flow regime were selected for analysis: (1) overall flow variability, (2) pattern of the flood regime, and (3) extent of intermittent conditions. From these three cateogries, 11 summary statistics were derived from the entire record for each stream (Table 1 and Appendix).

Overall flow variability

Three measures of flow variability were used. Mean annual coefficient of variation (ANNCV) assessed overall variability, although it was insensitive to temporal pattern in that it measures only degree of variation about the mean. The predictability aspect of overall flow variation was assessed with Colwell's

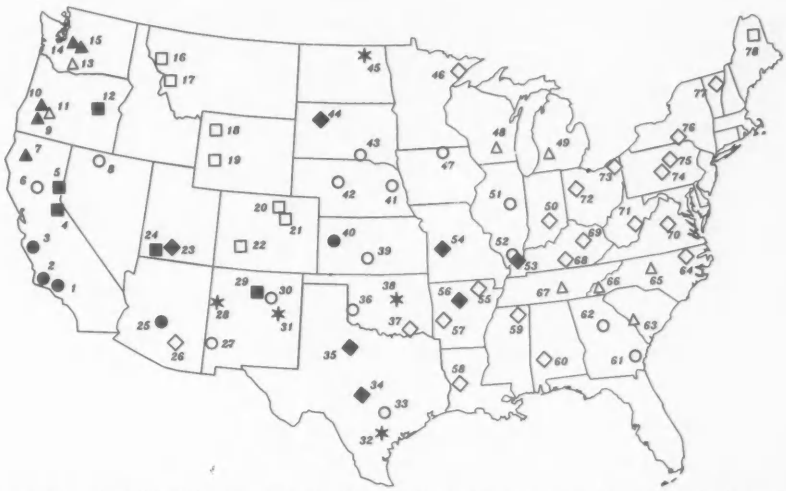

FIG. 1. Location of the 78 streams. Names (by map No.) and summary data are provided in Appendix. Symbols are cluster affiliation and are explained in legend to Fig. 2.

TABLE 1. Definitions for the 15 variables (in four categories) used in the analysis. Refer to text for further details and discussion.

Variable name	Definition
Basin descriptors	
AREA	Contributing watershed area (km^2) above location of stream gauge.
ANNQ	Mean annual flow ($m^3 \cdot s^{-1}$) of untransformed flow values over the period of record.
Q/AREA	ANNQ divided by AREA ($mm \cdot yr^{-1}$). Size scalar for streams.
LNANNQ	Grand mean flow of the ln-transformed flow.
Overall flow variability	
PREDQ	Colwell's (1974) predictability for all 24-h mean flows over the period of record. ($0 < PREDQ < 1$)
C/P	Proportion of total predictability (PREDQ) comprised by constancy (C). ($1.0 - C/P =$ proportion comprised by contingency.)
ANNCV	Mean annual coefficient of variation. The average over all years of the mean flow divided by the standard deviation times 100.
Pattern of the flood regime	
FLODFREQ	Flood frequency (number of floods$\cdot yr^{-1}$)
FLODINT	Median interval (d) between floods.
FLODDUR	Mean duration (d) of floods.
FLOD60D	Index of flood predictability. Maximum proportion of total number of floods over record that occur in any common 60-d period over all years in the period of record.
FLODFREE	Index of flood predictability. Maximum number of 365 d common to all years during which floods have not occurred.
FLODTIME	Median day among all days of the water year (beginning on Oct. 1) on which floods have occurred over the period of record.
Extent of intermittency	
ZERODAY	Average annual number of zero flow days.
LOWFLOW	Average over all years of the annual 24-h low flow value divided by the grand mean flow of the ln-modularized data.

(1974) measure of predictability for periodic phenomena, a measure of temporal uncertainty for some environmental state (here, daily streamflow). Predictability (PREDQ) ranges in value from 0 to 1 and is composed of two additive components: constancy (C), a measure of temporal invariance, and contingency (M), a measure of periodicity. For example, a springbrook with fairly uniform flow may have a predictability value near 1, nearly 100% of which is due to the constancy component (i.e. C/P proportion is high). In contrast, the high predictability of a stream having highly variable flow with a fixed periodicity would be due mostly to contingency. (Refer to Colwell (1974) for a complete description.) In this paper, the environmental state variable (flow) was divided into categories partitioned at 0.1, 0.25, 0.50, 0.75, 1.00 (mean), 1.25, 1.50, 1.75, 2.00, and 2.25 that spanned the entire range of modularized, ln-transformed daily flow values for all streams combined. The temporal unit used was 1 d, i.e. the daily flow state (24-hr mean discharge) for a stream was recorded for each day of a water year. This was repeated for all years of record so that the entire data set for each stream was contained in an 11 discharge category by 365 d matrix. (For leap years, day 366 of the water year (September 30) was deleted.) Each row in the matrix thus summed to the number of years in the record. The selection of a standard temporal unit is arbitrary and will influence the derived predictability values. We chose the daily unit because it allowed utilization of all available information in the record. Also, it was sensitive to sudden flow changes that might otherwise have been obscured by averaging over longer time intervals.

Pattern of the flood regime

Floods occur when flow fills an alluvial channel at bankfull discharge (Leopold 1962; Leopold et al. 1964). This level of flow is usually considered a formative, channel-modifying event (Richards 1982) during which significant substratum movement occurs (both suspended in the water column and moving along the bottom as bed load). We consider significant substratum movement to satisfy objectively Sousa's (1984) criterion for disturbance. Return periods for bankfull discharge can vary from 1–10 yr for different streams depending on basin area,

TABLE 2. Matrix of Pearson correlation coefficients for 15 variables (in four categories) on 78 streams.

	AREA	ANNQ	Q/AREA	LNANNQ	ANNCV	PREDQ	C/P	FLODFREQ
AREA	1.00							
ANNQ	0.04	1.00						
Q/AREA	−0.36[a]	0.40[a]	1.00					
LNANNQ	−0.04	0.84[b]	0.55[b]	1.00				
ANNCV	0.12	−0.39[a]	−0.39[a]	−0.47[a]	1.00			
PREDQ	−0.21	0.34[a]	0.50[b]	0.61[b]	−0.59[b]	1.00		
C/P	−0.12	0.29[a]	0.21	0.49[b]	−0.52[b]	0.64[b]	1.00	
FLODFREQ	0.22[a]	−0.17	−0.38[a]	−0.24[a]	0.31[b]	−0.45[a]	−0.30[a]	1.00
FLODINT	−0.30[a]	0.14	0.41[a]	−0.24[a]	−0.17	0.40[a]	0.12	−0.79[b]
FLOD60D	−0.06	−0.07	0.10	−0.03	0.04	0.29[a]	−0.20	−0.16
FLODFREE	−0.02	−0.14	0.09	−0.08	0.04	0.23[a]	−0.12	−0.02
FLODDUR	0.10	−0.15	−0.15	−0.14	0.04	0.22[a]	0.00	−0.01
FLODTIME	0.28[a]	−0.19	−0.55[b]	−0.19	0.31[a]	−0.09	−0.09	0.05
ZEROFLOW	0.21	−0.32[a]	−0.32[a]	−0.31[a]	0.92[b]	−0.36[a]	−0.29[a]	0.22
LOWFLOW	−0.15	0.34[a]	0.38[a]	0.57[b]	−0.81[b]	0.48[b]	0.79[b]	−0.34[a]

	FLODINT	FLOD60D	FLODFREE	FLODDUR	FLODTIME	ZEROFLOW	LOWFLOW
FLODINT	1.00						
FLOD60D	0.20	1.00					
FLODFREE	0.04	0.75[b]	1.00				
FLODDUR	−0.06	0.58[b]	0.40[a]	1.00			
FLODTIME	−0.04	0.20	0.14	0.28[a]	1.00		
ZEROFLOW	−0.10	0.08	0.03	0.10	0.21	1.00	
LOWFLOW	0.22[a]	0.08	0.11	0.13	−0.11	−0.61[b]	1.00

[a] $p<j0.05$.
[b] $p<0.01$.

sediment character, basin geomorphology, channel slope, and channel entrenchment (Richards 1982). However, the associated return periods for the discharge level effective in moving the greatest quantity of substratum range in the briefer interval of 1–3 yr (Richards 1982). Therefore, the effective flow for moving substratum is generally less than or equal to bankfull discharge. Leopold et al. (1964) give the average return period for bankfull discharge as 1–2 yr, which results in an average return time of 1.5 yr, a figure often used (e.g. Newbury 1984). We chose to use a more conservative flood value corresponding to a return period of 2 yr for the bankfull discharge.

Flood-level flow was calculated for each stream as follows. Annual 24-hr peak flows for the entire period of record were ranked and plotted on lognormal probability paper (using MINITAB) and a coefficient of determination (r^2) calculated for the regression line (cf. Morisawa 1968). The flow value corresponding to the 50% exceedence probability (2-yr return interval) was then chosen as the threshold flood value for that stream. Division by the grand mean modularized the value. The high r^2 values resulting from this analysis (Appendix) justified the use of the lognormal versus other distributions (see Richards 1982). An important assumption we made was that all flows exceeding these threshold flood values were qualitatively similar because the streams were at "bankfull discharge," i.e. the energy associated with the additional flow was expended outside the channel. (It is also important to note that use of annual mean 24-hr peak flow rather than instantaneous flow in the ranking procedure results in a consistent underestimation of actual bankfull discharge. This will be particularly true for streams that flood for only minutes during a day (e.g. see Minckley and Meffe 1987). However, because available long-term daily flow records consist of 24-hr means, rather than instantaneous values, it is necessary to define floods using the peak 24-hr mean. This technique thus measures an index of bankfull discharge.)

After establishing a threshold value for a stream-specific flood-disturbance, the flood regime for the entire period of record was evaluated with respect to six derived variables (Table 1). Flood frequency (FLODFREQ) was the mean number of floods per year over the period of record. Floods lasting more than 1 d counted as one flood. The intervals in days between floods were computed and the median determined (FLODINT). When the interval between two consecutive floods was 2 d or less, the floods were typically combined into one event. For those streams having floods clearly resulting from seasonal snowmelt (based on observation of the timing and duration of all floods in the record), the cutoff interval was relaxed to 8 d because flow conditions during these intervals were high but just below the prescribed flood threshold value. The mean duration for floods (FLODDUR), a possible index of disturbance intensity, was calculated by considering how many days each flood lasted. The predictability of flooding was assessed with two indices. By determining the day of the water year (October 1–September 30) on which each flood occurred, the temporal distribution of floods in a stream could be evaluated. The maximum proportion of all floods falling in any 60-d period common to all years in the record was determined to provide an index of flood predicatability (FLOD60D). Similarly, the maximum number of 365 d over all water years during which no floods occurred (FLODFREE) also characterized predictability of flooding. An index of seasonality (FLODTIME) was considered by determining the median day (of the water year) among all days on which floods occurred over the entire period of record.

Extent of intermittent conditions

Intermittency was evaluated by determining the average annual number of zero flow days for each stream (ZERODAY).

TABLE 3. Numerical means and standard deviations (in parentheses) of 11 variables for nine clusters.

	Harsh intermittent[a]	Intermittent flashy	Intermittent runoff	Perennial flashy	Perennial runoff	Winter rain	Snow + rain	Snowmelt	Mesic groundwater
ANNCV	151.3	88.3	68.2	24.2	31.4	20.7	26.4	27.5	10.5
	(37.4)	(25.9)	(22.0)	(11.9)	(7.5)	(8.6)	(11.2)	(9.3)	(6.1)
PREDQ	0.29	0.24	0.25	0.49	0.44	0.67	0.56	0.69	0.72
	(0.07)	(0.07)	(0.06)	(0.17)	(0.09)	(0.11)	(0.11)	(0.11)	(0.08)
C/P	0.54	0.30	0.32	0.80	0.69	0.70	0.66	0.61	0.89
	(0.20)	(0.11)	(0.13)	(0.14)	(0.12)	(0.11)	(0.14)	(0.13)	(0.08)
FLODFREQ	0.87	1.21	0.81	1.01	0.75	0.77	0.86	0.69	0.63
	(0.12)	(0.07)	(0.08)	(0.14)	(0.09)	(0.11)	(0.09)	(0.08)	(0.09)
FLODINT	263	47	342	144	304	299	263	361	414
	(62)	(14)	(81)	(85)	(71)	(106)	(105)	(15)	(104)
FLOD60D	0.59	0.61	0.55	0.46	0.48	0.65	0.74	0.94	0.51
	(0.09)	(0.09)	(0.15)	(0.07)	(0.11)	(0.09)	(0.05)	(0.07)	(0.08)
FLODFREE	124	192	136	132	101	226	172	273	131
	(65)	(36)	(66)	(56)	(49)	(49)	(33)	(53)	(35)
FLODDUR	2.5	2.3	2.3	3.0	1.6	1.9	12.7	7.2	2.2
	(2.0)	(0.4)	(1.6)	(1.8)	(0.6)	(0.4)	(3.1)	(3.3)	(1.7)
FLODTIME	236	159	207	211	163	99	209	242	149
	(45)	(64)	(34)	(50)	(22)	(16)	(27)	(17)	(41)
ZEROFLOW	96.2	32.6	17.0	0.1	0.1	0	0.2	0	0
	(17.0)	(16.3)	(11.4)	(0.4)	(0.4)	(0)	(0.4)	(0)	(0)
LOWFLOW	0.02	0.10	0.14	0.61	0.45	0.66	0.46	0.66	.83
	(0.02)	(0.05)	(0.12)	(0.20)	(0.14)	(0.16)	(0.13)	(0.09)	(0.08)

[a]Scores exclusive of Mauvis Coulee, North Dakota, which was added a posteriori to this group.

An additional index of intermittency (LOWFLOW) was calculated as the mean of all the annual low flow values divided by the grand mean discharge. Thus, streams with potentially biologically significant low flow periods that approached but did not reach zero were assessed by this variable.

Analysis and Results

Cluster Analysis of Streamflow Pattern

One objective of the analysis was to determine similarities with respect to flow regime among the 78 streams. A descriptive cluster analysis approach that was exploratory and made no distributional assumptions that would justify statistical inferences was adopted. Because we were interested in examining similarity between streams based on variables derived from the daily flow records, the four basin descriptors (AREA, ANNQ, Q/AREA, and LNANNQ) were deleted from the cluster analysis (but see below for a check on this procedure).

First, inspection of all pairwise plots of variables across all streams revealed that the relationships between almost all pairs were no higher than first-order. Therefore, the strengths of linear association among variables were assessed (on BMDP) using Pearson correlation coefficient, r (Table 2). Many of the derived variables were significantly correlated with one another, due both to the large sample sizes and the inherent interdependency between flow-related variables. However, the generally low r values in Table 2 indicate that much variability existed in the relationship between most variables. For example, PREDQ and ANNCV, temporal and nontemporal measures of overall flow variability, respectively, correlated differentially with measures of the flood regime. Both variables showed some association with flood frequency (FLODFREQ and FLODINT), but only PREDQ showed nonzero correlation with the other aspects of the flood regime, viz. flood predictability (FLOD60D and FLODFREE) and flood duration (FLODDUR). Thus, single measures of overall flow variability (i.e. PREDQ and ANNCV) generally could explain very little of the variability in flood disturbance characteristics.

For the cluster analysis, a nonhierarchical classification scheme (BMDP K-means) was utilized. Nonhierarchical clustering was a useful approach for exploring initial relationships between samples (here, streams) that shared similarities in measured characteristics (here, 11 derived streamflow variables) (Gauch 1982). Because resultant clusters had no joint structure, statistical inferences concerning differences between clusters were not appropriate. However, cluster designations suggested hypotheses that could be subjected to additional multivariate techniques (Gauch 1982). Values of the 11 derived streamflow variables for each stream were used as input. Because of the differences in the magnitudes in the units, variables were standardized by dividing the value of each variable by the standard deviation of that variable. The classification routine assigned each sample (stream) to one of the K user-defined clusters based on minimum Euclidean distance (in variable space) between the sample and the centers of all clusters. The number of clusters specified in nonhierarchical cluster analysis was arbitrary. After several runs, we chose nine clusters because this number optimized group separation and interpretation. Table 3 gives the cluster mean and standard deviation for each variable for each of the nine groups.

The nine clusters could be grouped broadly into intermittent and perennial streams. Among the former, harsh intermittent streams were characterized by long periods of zero flow and by very low flow each year. They tended to occur in the arid to semi-arid southwest (Fig. 1), with the exception of one stream, which was placed a posteriori into the harsh intermittent group (see Table 3, Appendix). Streams with long periods of

intermittency could, however, also occur in more mesic, eastern regions (see Williams and Hynes 1976; Delucchi 1988). Two additional groups of intermittent streams had a moderate degree of zero flow and low flow conditions. Intermittent flashy streams had a high frequency of floods that were moderately seasonal in their distribution. They occurred generally in the arid southwest, where vegetation cover in the watersheds is sparse and precipitation is seasonal. Members of the intermittent runoff group were located in the more semi-arid central United States. They flooded less frequently and less predictably, perhaps due to relatively more watershed vegetation cover and less seasonal precipitation patterns. All three groups of intermittent streams were characterized by high variability and low predictability of flow.

Perennial streams had no more than occasional zero flow days (Table 3). The perennial flashy group was characterized by a high frequency of nonseasonal flooding. They tended to occur in the arid to semi-arid regions of the United States and to be maintained by subsurface flow (note low ANNCV and high C/P in Table 3). Perennial runoff streams, which generally occurred in the more heavily-vegetated, mesic regions (Fig. 1), flooded less frequently and appeared to be less influenced by subsurface flow. The one desert stream in this group shared similar temporal characteristics (e.g. PREDQ, FLOD60D, FLODFREE — see Appendix) with the geographically proximate intermittent flashy group, but its flow constancy (e.g. C/P, LOWFLOW) imparted characteristics that caused it to cluster differently.

The winter rain streams of the Pacific Northwest were characterized by intermediate flood frequency and medium to high seasonality of flow and flooding. The median time for floods (FLODTIME) in this group was day 99 or early January (Table 3). The mesic groundwater streams, most temporally constant of all groups with respect to flow variation, were similar to the winter rain streams except that they flooded relatively infrequently and less seasonally than did the latter. They were generally eastern in distribution, with the exception of two Pacific Northwest members, one of which was actually a lake outlet stream and thus had high flow constancy and lower flood frequency (see Appendix).

The final two groups were clearly influenced by seasonal snowmelt. Snowmelt streams flooded very predictably; however, depending on annual snowpack and vernal weather conditions, they did not necessarily flood every year. They had low variability and high predictability of flow. All but one were western montane systems. The snow + rain group also consists of western montane streams that differ from the previous group in their greater flood frequency, lesser (but still relatively high) flood predictability and lesser flow predictability. These watersheds appeared to be influenced not only by annual snowfall, but by seasonal rainfall patterns as well. Interestingly, flood duration (FLODDUR) was high for these two stream groups (Table 3), but for no others. This variable, therefore, did not provide additional separation between stream types.

Streamflow Clusters versus Alternative Variables

To address the possibility that the nine clusters could have been described from the four discarded basin descriptors, a MANOVA ($k=9$ clusters, $p=4$ variables, $n=78$ streams) was run on SPSSX. Although the correlation between the individual basin descriptors and each of the 11 derived streamflow variables was generally low (Table 2), the inherent correlation structure between these four variables and the original 11 restricted hypothesis tests of mean differences between clusters (i.e. because clusters were generated using variables correlated to these four). However, analysis of variance could be used to describe (as opposed to test) the differences between the established clusters with respect to the four variables (P. Chapman, Department of Statistics, Colorado State University, pers. comm.). Computed statistics and associated p-values could be used to suggest differences between groups. In the MANOVA each of the 78 streams was coded according to its cluster affiliation. Using AREA, Q/AREA, ANNQ, and LNANNQ as variables, the established clusters appeared to differ with respect to the four basin descriptors (Wilk's $\lambda=0.42$, $p<0.001$). Examination of the univariate F-tests further suggested that Q/AREA was the only variable responsible for the difference between clusters ($F=3.94$, $p<0.001$). Visual inspections of central tendency and range of values for Q/AREA in each established cluster revealed that winter rain streams had very high values, harsh intermittent streams had very low values, and all other stream categories were intermediate and overlapping in value. (This same trend, though less pronounced, was observed for LNANNQ and ANNQ as well.) In conclusion, the four discarded basin variables could not satisfactorily separate the 78 streams into the nine clusters established from the derived streamflow variables.

Discussion

Implications for Community Structure

Disturbance (floods and intermittency) and flow variability interact to provide a complex physical template (sensu Southwood 1977, 1988) that can influence population and community patterns of stream organisms. Clearly, the relative contributions of these hydrologic variables to the overall selective forces in streams are themselves temporally variable and thus conceptually difficult to disentangle. The recognition that streamflow environments are more appropriately considered as arrayed continuously along axes of hydrologic variability, not as discreet units or clusters, further emphasizes this point. Some combination of flood frequency (FLODFREQ and FLODINT), flood predictability (FLOD60D and FLODFREE), and overall flow variability (temporal PREDQ or nontemporal ANNCV) are likely contributors to the physical templates in all but the harsh intermittent streams. Therefore, these hydrologic components can be argued to interact to establish a significant portion of the gross physical flow template in most streams (and thereby to delimit the range of biotic responses and interactions). By viewing all 78 streams in the space generated by these three components (Fig. 2), a sense of the range of ecologically important hydrologic variability for a large number of North American streams is achieved. (Although this representation excludes the intermittency axis, note that intermittent streams are included in the figure.

To assess the relative contributions of various components of streamflow variability to a stream's physical flow template, a conceptual model that incorporates the nine clusters can be constructed (Fig. 3). Hydrological variables can be hierarchically ranked as follows, according to the order of their importance in defining a stream's flow template: degree of intermittency, flood frequency, flood predictability, and overall flow predictability/variability.

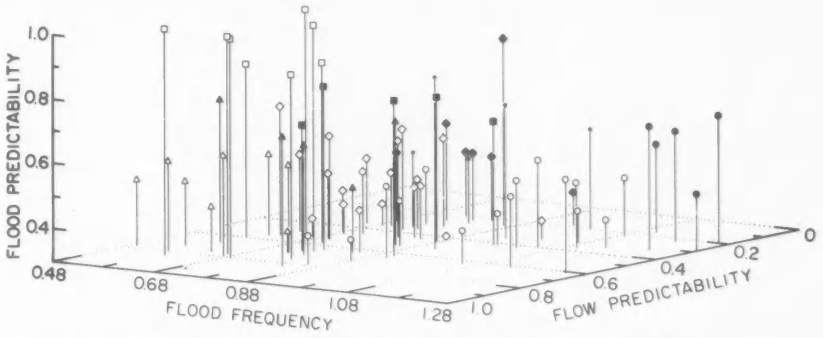

FIG. 2. Plot of the 78 streams (coded by cluster) showing wide distribution in three-variable space defined by flood frequency (FLOD-FREQ), flood predictability (FLOD60D), and overall predictability of flow (PREDQ). Note that intermittent streams are included though an intermittency axis is excluded. (★ = harsh intermittent, ● = intermittent flashy, = intermittent runoff, ○ = perennial flashy, ◇ = perennial runoff, ▲ = winter rain, □ = snowmelt, ■ = snow + rain, Δ = mesic groundwater.)

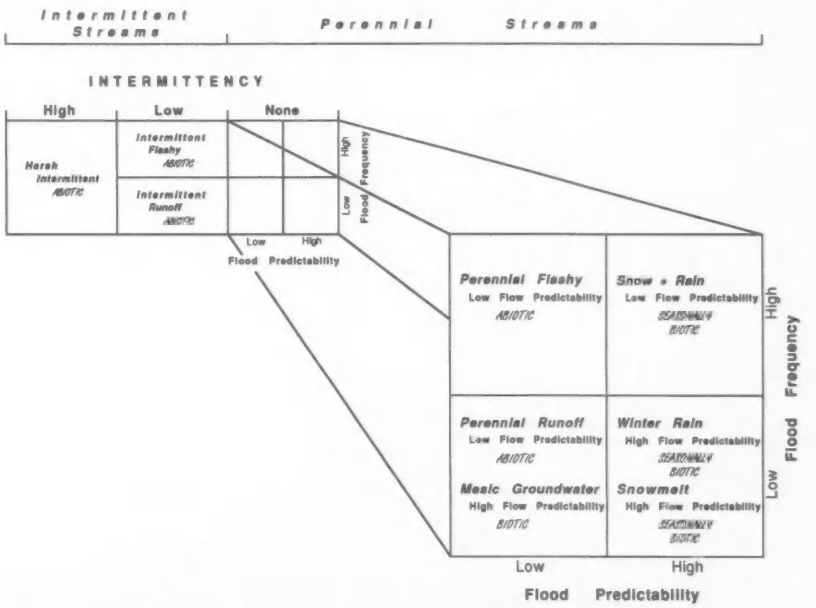

FIG. 3. Conceptual model of classification of stream clusters based on hierarchical ranking of four temporal components of discharge regime. The degree of intermittency is the first variable of consideration. For streams with low intermittency and for perennial streams, flood frequency is a variable separating stream types. For perennial streams flood predictability must also be considered. Overall flow predictability (irrespective of disturbance regime) is generally important only within certain combinations of flood frequency and predictability in perennial streams. Combinations of hydrologic variables result in streamflow templates in which the relative contributions to community structure of abiotic and biotic processes are expected to differ, as indicated. See text for more complete discussion.

The premise underlying the following discussion is that highly variable and/or unpredictable flow regimes provide a physical template in which abiotic processes are of predominant importance in controlling lotic processes and contributing to observed ecological patterns, whereas more benign or predictable flow environments are conducive to the development of stronger biotic interactions such as competition or predation, which can directly influence observed pattern (cf. Sanders 1969; Fisher 1983; Peckarsky 1983; Ward and Stanford 1983; Reice 1985; Ross et al. 1985; Walde 1986; Resh et al. 1988). However, in many if not most lotic systems, streamflow regimes are intermediate between these extremes such that both abiotic and biotic factors contribute to community structure at various times (Matthews 1988; Minshall 1988; Power et al. 1988; also cf. Menge and Sutherland 1987; Southwood 1988).

Ecological attributes that reflect streamflow environment are considered at the population and community levels of organization. Life history characteristics and other population

TABLE 4. Potential biological attributes in lotic habitats as four independently-considered hydrological factors increase in magnitude. See text for further development and appropriate references.

Hydrologic factors	Biological attributes	
	Population	Community
Intermittency	Inverts: Diapause/aestivation Desiccation avoidance behavior Increasing dispersal capability Fish: Small body size Upstream migrations following resumption of flow Increased physiological eurytopy	Trophically simple Richness: Low relative to regional species pool Stability and persistence: High due to drought-selected taxa Succession: Autogenic forces predominant (due to seasonal flow reduction) High predictability of trajectory after resumption of flow Community Structure: Abiotic factors predominant
Flood frequency	Inverts: Small body size Accelerated and asynchronous development Behavioral avoidance of floods Fish: Small body size Fusiform shape favored Behavioral avoidance of floods Low recruitment, uneven age distribution	Trophically simple Richness: Low relative to regional species pool Stability and persistence: Increases due to flood-selected taxa Succession: Allogenic forces predominant Poor development following floods; limited species replacements Community structure: Abiotic factors predominant
Flood predictability	Inverts: Increased developmental synchrony Emergence/reproduction temporally cued to flood(s) Fish: Larger body size, more specialists Behavioral and/or life history avoidance of floods High recruitment, more even age distribution	Trophically complex Richness: Intermediate relative to regional pool Stability and persistence: Increases due to flood-adaptations Succession: Autogenic forces predominant; increasing predictability of trajectory Community structure: Biotic factors predominant seasonally
Flow predictability	Inverts: Larger body size, more specialists Increasing proportion long-lived species Developmental synchrony variable Fish: Larger and more specialists Increasing proportion of long-lived species High recruitment, more even age distribution	Trophically complex Richness: High relative to regional species pool Stability and persistence: Decreases due to flood-prone species Secondary succession: Autogenic forces predominant Strong development following floods; timing of flood yields unpredictable path Community structure: Biotic factors predominant

characteristics can vary within the same species inhabiting qualitatively different habitats as a function of habitat-related selective forces (Tinkle and Ballinger 1972; Southwood 1977; Hornbach and Childers 1986; Petranka et al. 1987; Willows 1987; see also Begon et al. 1986, chapter 14). Moreover, there is an increasing body of evidence suggesting local population adaptation not only to absolute environmental variables but to the degree of environmental variation as well (Nichols et al. 1976; Leggett and Carscadden 1978; Vepsäläinen 1978; Diamond 1982; Dingle 1984; McLachlan 1985; Kaitala 1987; Etter 1988). Qualitative trends toward some local optimum life history attributes within species' adaptative constraints (cf. Levins 1968) may be observable, particularly for local populations inhabiting streams of differing flow patterns within relatively close geographic proximity. At the community level, persistence and stability (sensu Connell and Sousa 1983) and succession (sensu Fisher 1983) are considered.

The following discussion is largely speculative given the virtual absence of empirical data on stream organisms that correspond to the available long-term flow data. It is intended primarily to suggest possible fruitful areas of focus in relating hydrological pattern to ecological process and pattern (see Resh et al. 1988 for other speculative suggestions). The summary in Table 4 should be referred to throughout the discussion.

Streams that experience prolonged periods of intermittency (e.g. harsh intermittent) present special physiological and life

history problems to the flora and fauna when compared with perennial streams. Long periods of zero flow conditions may provide selective pressure for specific life history characteristics such as invertebrate aestivation and egg diapause (Williams and Hynes 1977), high vagility among fishes (Larimore et al. 1959), and physiological tolerance to low dissolved oxygen (Williams and Hynes 1977; Matthews 1987) and may eliminate poorly-adapted colonizing taxa (Delucchi 1988). These characteristics may lead to such community attributes as high persistence and stability and relatively high predictability of successional patterns following the seasonal resumption of flow (Table 4), although these attributes can vary depending on the duration of drying, the time since drying and the distance from recolonization sources (cf. Iversen et al. 1978; Delucchi 1988, 1989). Other hydrological characteristics (flood frequency, flood predictability, overall flow predictability) should be of secondary importance in these streams. In general, biotic interactions should contribute relatively little to community structure given the demanding environment.

As intermittency becomes less prolonged (e.g. in intermittent flashy and intermittent runoff streams), other hydrologic forces such as floods become increasingly important in influencing community structure (cf. Stehr and Branson 1938; Harrel and Dorris 1968). Floods are widely viewed as reset mechanisms (Fisher 1983; Cummins et al. 1984; Minshall et al. 1985b; Resh et al. 1988), and flood-related mortality to lotic organisms can result either directly from scouring, crushing, or downstream export of individuals (e.g. Thorup 1970; Power and Stewart 1987; Minckley and Meffe 1987) or indirectly from food resource loss (Hanson and Waters 1974). In streams that both flood frequently and dry annually, animals may possess life history characteristics for both flood and desiccation avoidance. For example, insects of Sycamore Creek in Arizona have presumably adapted to the flood regime of high frequency through accelerated developmental rates that reduce the time larvae spend in the stream and that allow adults to recolonize quickly through oviposition following flooding (Gray 1981; Fisher et al. 1982). Rapid development and habitat selection by ovipositing adults enhance persistence through intermittent conditions. Trends toward increased developmental rate, decreased developmental synchrony, and reduced body size may be generalized responses of aquatic insects to increasing disturbance frequency (cf. Slobodkin 1968), particularly in warmer climatic regions where aerial adults can survive year-round. Also, in warm-water streams subject to both intermittency and frequent flooding, succession following disturbance can be pronounced for rapidly-reproducing species such as algae and insects (Fisher et al. 1982). In such systems, time since last flood can help explain community structure as well (Fisher and Grimm 1988). Because of life history adaptations to the disturbance regime (cf. Fisher et al. 1982) community persistence can also be high in such streams.

Where streamflow is perennial (i.e. the remaining six clusters), components of the flood regime, particularly the interaction of frequency (FLODFREQ and FLODINT) and predictability (FLOD60D and FLODFREE) are likely of primary significance in structuring lotic communities. If flood frequency is high, the relative contributions of biotic interactions to community structure are likely to depend on the temporal pattern of the flood regime. Overall flow predictability (PREDQ) and variability (ANNCV) are likely to attain relative importance in describing a stream's flow template only under certain combinations of flood frequency and flood predictability (Fig. 3). As flood frequency increases, selection pressure is presumably exerted for certain behavioral and life history characteristics that maintain population persistence or homeostasis (cf. Slobodkin 1968) (see Table 4). For example, some invertebrates actively migrate either into the substratum (Zahar 1951) or to quieter backwaters (Lehmkuhl and Anderson 1972) to avoid spates. Fish avoidance behavior may reflect evolutionary history with frequent floods (Meffe 1984). Populations from streams with high flood frequency can be characterized by small, vagile and/or colonizing assemblages of invertebrates (e.g. Siegfried and Knight 1977) and of fish (e.g. Harrell 1978; Schlosser 1985, 1987; Meffe and Minckley 1987). The population densities of such species can fluctuate as a response to floods, but persistence can be high (e.g. Matthews 1986; Meffe and Minckley 1987; Meffe and Berra 1988). The most persistent fish species are likely to be those possessing a morphology favorable to surviving flood flows (e.g. Schlosser 1985; Matthews 1986; Minckley and Meffe 1987). Floods have been shown to regulate community structure by facilitating local coexistence between asymetrically-competitive algal species (Power and Stewart 1987) and invertebrate species (Hemphill and Cooper 1983; McAuliffe 1984) and between an exotic fish predator and its native, relatively flood-resistant prey (Meffe 1984).

The importance of high flood frequency can be tempered somewhat by high flood predictability because of potential, evolutionary-mediated life history adjustments to this predictability (Huston 1979; Thiery 1982) (Table 4). Moyle and Vondracek (1985) suggested that the high predictability of nonflood periods in montane western streams serves as a reliable environmental cue for native salmonid species, whose flood-susceptible fry are present only during the flood-free summer season. Similarly, John (1963, 1964) found that cyprinid life histories in the desert southwest are linked to the timing of floods, which can be used as reproductive cues. Gray (1981) suggested that some insects' reproductive activities may be adjusted to a largely seasonal flood regime.

Conditions of high flood frequency and low flood predictability (e.g. in perennial flashy streams), are likely to minimize the contributions of biotic interactions to community structure over long time scales. However, in years when periods between floods are long and overall flow conditions are relatively invariant (see C/P in Table 3), biotic interactions might become sporadically important, particularly for species with short generation times. Brier Creek, a perennial stream in southern Oklahoma with late summer low flow, perhaps falls into this category. Extensive research on this system has shown that floods are an important structuring agent in this stream, but that biotic factors such as competition and predation can also contribute to community structure during periods of flow constancy (reviewed in Matthews 1988).

Where high frequency is coupled with relatively high predictability of flooding (e.g. snow + rain streams) biotic interactions should attain relative importance, at least seasonally between floods (cf. Minshall et al. 1985a; Moyle and Vondracek 1985). Although floods typically occur in late spring in snow + rain streams (see FLODTIME in Table 3), in some years winter rains cause severe early season flooding (Erman et al. 1988). Winter floods in Sagehen Creek tend to reduce egg survival and adult densities of native brook trout (and sculpins) (Erman 1986; Erman et al. 1988), to such an extent that fry of nonnative, spring-spawning rainbow trout are able to compete successfully with brook trout fry in the late spring (Seegrist and

Gard 1972). However, because the flood-free season is long and coincides with the period of recruitment and growth, fish assemblage persistence and stability can be high on a year-to-year basis in these and other snowmelt streams (Moyle and Vondracek 1985; Erman 1986). (Interestingly, intermittent flashy streams are also characterized by a high flood frequency and a moderately high flood predictability (Table 3). Biotic interactive strength might therefore be enhanced during the flood-free season; however, this season is coincident with the period of stream intermittency, which would minimize the contributions of biotic interactions to community structure).

For streams with low flood frequency, the importance of biotic interactions may reflect not only flood predictability, but overall flow predictability/variability as well. Snowmelt and winter rain streams have relatively high flood predictability (Table 3, Fig. 3) and thus would be expected to provide environments conducive to the expression of strong biotic interactions, at least seasonally (cf. Minshall et al. 1985a). The relatively high overall flow predictability (low variability) in these streams should further enhance this expression (Table 4). Succession in these streams should be relatively predictable given the seasonal nature of the flood regime.

Perennial runoff and mesic groundwater streams have typically low flood predictability coupled with low flood frequency, but they differ from one another with respect to overall flow predictability (Table 3, Fig. 2). Perennial runoff streams generally have low overall flow predictability; therefore, abiotic processes are likely to predominate in such lotic systems. High flow variability can reduce the consistency of biotic interactions by frequently upsetting current-related resource and microhabitat distributions (Reice 1985; Schlosser and Toth 1984; Bain et al. 1988; Power et al. 1988) and perhaps by requiring individuals to make physiological adjustments to changing physico–chemical conditions (cf. Slobodkin 1968; Slobodkin and Sanders 1969). However, during periods of low flow, and the attendant reduction of habitat area or volume, biotic interactive strength could become temporarily important (cf. Matthews 1988), particularly if habitat reduction and crowding were not so great as to induce physiological and behavioral stress. Succession in these streams is not likely to be strongly developed or detectable due to the relatively unpredictable and variable nature of the flow regime (cf. Fisher and Grimm 1988). Community persistence, however, may be great given the presumed adaptedness of the fauna to environmental variability (cf. Matthews 1986). (Intermittent runoff streams, slightly more variable than perennial runoff streams and with only a few zero flow days per year (Table 3, Fig. 3) might also exhibit these characteristics).

Mesic groundwater streams flood relatively infrequently and have very high overall flow predictability due largely to flow constancy (Table 3). Strong biotic interactions and successional patterns should be relatively well-developed in such streams (cf. Fisher 1983) (Table 4). However, these streams should also be relatively vulnerable to disturbance from temporally unpredictable floods. If, for example, a stream has not been flooded for a long time, "late-succesional" species can show low resilience (e.g. Harrell 1978) or species in vulnerable life history stages (e.g. Thorup 1970) can be greatly reduced in abundance. Thus, the time since the last flood (see Fisher et al. 1982; Fisher 1983, 1987) becomes a critical consideration in community analysis for streams of this type.

Prospectus

Long-term studies and carefully-defined experiments will be necessary to evaluate hypotheses about the broad-scale importance of hydrologic variability on lotic community structure (cf. Callahan 1984). As Schlosser (1987) points out, detecting fish assemblage persistence of shifts in community structure requires multi-year sampling efforts due to between-year variation in environmental conditions and associated ecological processes such as recruitment, age structure, habitat partitioning, and species composition. These same constraints hold for invertebrate assemblages as well.

Conclusion

We believe that the comparative analysis of long-term daily flow records for these 78 widely-distributed streams provides a context in which to evaluate the relative variability of any particular stream's streamflow environment. Given a sufficient record and the statistics that can be derived from it, a stream can be clustered in 11-dimensional flow space (Table 3, Fig. 1) and summarized in four-dimensional (Fig. 3) or arrayed in continuous three-dimensional (Fig. 2) flow space, the axes of which correspond to indices of flow variability having documented ecological significance. The position of a stream in flow space should provide some a priori basis for expectations of relative biotic attributes (both in terms of population and community processes and patterns) that may characterize these streams, all else being equal. However, as all else is never equal on such a broad spatial scale, this streamflow characterization should only be viewed as one conceptual framework that demonstrates the range of streamflow variability and that provides a more objective basis for expectation of ecological attributes (for another see Resh et al. 1988). Although in need of refinement to meet local conditions, our characterization of patterns of temporal hydrographic variation should nevertheless contribute to the development of more quantitative, objective criteria for assessing the relative importance of flow variability and disturbance in structuring stream communities (cf. Wiens 1984). Such criteria are needed for the eventual rigorous linkage of ecological with hydrological data. Also needed, however, is more effort toward assembling long-term biological datasets from streams with reliable long-term flow records.

There is a continuing concern among stream ecologists to relate community pattern and process to environmental variation, including streamflow (Matthews and Heins 1987; Covich 1988; Matthews 1988; Minshall 1988; Power et al. 1988; Resh et al. 1988). Our analysis demonstrates that long-term, daily streamflow records are rich sources of information with which to evaluate temporal and spatial patterns of lotic environmental variability and disturbance across many physiographic and ecographic regions. Only with such a long-term and broad perspective can stream ecologists reliably determine the temporal and spatial scale(s) appropriate in generalizing patterns and processes in lotic communities.

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APPENDIX. Summary data for 78 streams.

State	Map[a] No.	Stream name	USGS Gauge No.	Years in record	AREA (km^2)	ANNQ ($m^3 \cdot s^{-1}$)	Q/AREA ($mm \cdot yr^{-1}$)	LNANNQ ($m^3 \cdot s^{-1}$)	Flood[b] ($m^3 \cdot s^{-1}$)
AL	60	Turkey Creek	02427700	28	253	4.1	435	1.0	98.0
AR	57	Cossatot River	07340300	17	232	5.4	742	2.0	132.3
	56	Big Piney Creek	07257000	35	710	11.5	502	2.4	256.0
	55	Piney Fork	07073500	45	257	2.5	313	0.8	65.7
AZ	26	Aravaipa Creek	09473000	20	1401	1.0	23	0.5	20.2
	25	Sycamore Creek	09510200	24	425	0.8	63	0.1	15.9
CA	2	Salsipuedes Creek	11132500	44	122	0.3	77	0.1	7.9
	4	Clark Fork Stanislous River	11292500	35	175	4.5	812	2.3	24.9
	5	Sagehen Creek	10343500	32	27	0.4	428	0.2	2.2
	6	Big Chico Creek	11384000	56	188	4.2	706	1.8	63.1
	7	Trinity River	11423200	29	386	12.2	999	5.6	104.1
	3	Arroyo Seco	11152000	84	633	4.8	244	0.8	93.3
	1	Sespe Creek	11113000	58	650	3.3	159	0.3	80.3
CO	22	East River	09112500	63	749	9.6	401	4.6	58.3
	20	Colorado River	09010500	30	138	1.8	414	0.7	13.5
	21	St. Vrain Creek	06724000	81	549	3.7	210	1.4	23.2
GA	62	Middle Ocone River	02217500	48	1031	15.0	454	10.3	160.0
	61	Satilla River	02226500	48	3108	29.7	294	9.5	213.8
IA	47	Winnebago River	05459500	53	1362	7.5	173	3.1	71.2
IL	53	Lusk Creek	03384450	18	111	1.8	516	0.3	58.9
	52	S.Fork Saline River	03382100	20	381	4.8	394	1.1	71.2
	51	Vermilion River	05554500	43	1500	11.2	232	2.8	133.6
IN	50	Youngs Creek	03362000	43	277	3.0	341	1.0	68.4
KS	39	Rattlesnake Creek	07142300	28	2030	1.0	15	0.5	8.6
	40	Smoky Hill River	06860000	46	9207	0.9	3	0.1	15.7
KY	69	Stoner Creek	03252000	31	619	8.2	418	1.9	187.7
	68	Russell Creek	03307000	46	487	8.3	541	2.8	173.3
LA	58	Bayou Toro	08025500	29	383	4.1	340	1.0	89.6
ME	78	Machias River	01016500	32	855	16.2	596	7.5	161.6
MI	49	Augusta Creek	04105700	21	101	1.2	381	1.2	3.3
MN	46	Baptism River	04014500	34	363	4.8	416	2.0	58.9
MO	54	Cedar Creek	06919500	37	1088	8.7	253	1.3	220.3
MS	59	Skuna River	07283000	38	658	10.7	510	1.6	294.4
MT	16	Prospect Creek	12390700	29	471	7.3	488	4.0	44.5
	17	M. Fork Rock Creek	12332000	48	319	3.5	345	1.9	23.7
NC	66	Little Tennessee River	03500000	40	363	11.2	972	9.1	78.7
	65	Hunting Creek	02118500	34	401	5.8	458	4.5	79.4
	64	Potecasi Creek	02053200	27	583	6.7	361	2.2	53.3
ND	45	Mauvis Coulee	05056100	26	1002	0.5	17	0.1	3.4
NE	42	Dismal River	06775900	20	2490	5.4	69	5.5	7.2
	41	Logan Creek	06799450	22	1890	4.4	74	2.5	95.2
NM	31	Conchas River	07222500	51	1018	0.4	12	0.1	19.2
	30	Gallinas River	08380500	61	218	0.5	79	0.3	4.2
	27	Gila River	09430500	59	490	2.8	182	2.6	36.1
	29	Pecos River	08378500	57	4828	4.2	27	1.6	13.3
	28	Zuni River	09386950	18	2098	0.4	6	0.1	6.9
NV	8	Martin Creek	10329500	65	446	1.0	69	0.5	6.4
NY	79	Owego Creek	01514000	48	479	7.9	522	3.3	118.5
OH	72	Conneaut Creek	04213000	24	453	7.6	530	3.1	141.9
	73	Auglaize River	04186500	45	834	8.1	296	2.5	131.0
OK	37	Blue River	07332500	50	1233	7.1	181	2.7	201.5
	36	Elm Fork N.F.Red River	07303400	20	1077	1.2	35	0.5	45.0
	38	Dry Creek	07243000	31	179	0.6	104	0.1	32.0
OR	9	S.Fork McKenzie River	14159200	28	414	18.2	1389	14.2	12.7
	10	Smith River	14158790	25	42	2.6	1974	1.3	22.5
	11	McKenzie River	14158500	41	239	13.4	1769	11.8	37.9
	12	Silvies River	10393500	65	2419	5.0	65	1.5	31.1
PA	74	Penns Creek	01555000	56	780	12.5	505	7.2	119.7
	75	Towanda Creek	01532000	71	554	8.2	469	3.0	152.2
SC	63	Upper Three Runs	02197300	18	225	3.0	424	3.0	8.0
SD	44	Moreau River	06359500	44	6890	3.8	18	0.6	82.7
	43	Keya Paha River	06464500	40	2771	2.0	23	1.2	17.0
TN	67	Duck River	03596000	52	277	5.2	596	2.3	127.1
TX	33	San Marcos River	08172000	46	2170	10.3	150	6.5	160.0
	34	Beaver Creek	08150800	24	557	0.5	27	0.1	30.7
	32	Ecleto Creek	08186500	25	619	1.0	53	0.1	50.1
	35	North Croton Creek	08082180	21	650	0.4	21	0.1	17.6
UT	24	E. Fork Virgin River	09404450	20	179	0.6	107	0.5	2.0
	23	Pine Creek	09337000	29	176	0.1	25	0.1	1.4
VA	70	Rapidan River	01665000	43	295	4.2	439	2.5	54.9
VT	77	Moose River	01134500	37	195	4.1	660	2.2	47.2
WA	13	White Salmon River	14121300	21	84	4.3	1620	3.9	14.2
	14	Newaukum Creek	12108500	32	71	1.7	772	1.3	12.1
	15	Green River	12104500	40	249	11.1	1401	6.5	99.0
WI	48	Black Earth Creek	05406500	31	118	0.9	243	0.8	7.4
WV	71	Williams River	03186500	56	332	9.4	896	4.3	122.1
WY	18	S.Fork Shoshone River	06280300	29	769	12.0	494	5.8	92.3
	19	East Fork River	09203000	48	205	2.9	452	0.8	31.3
Mean value				39	931	5.5	408	2.6	
Minimum value				17	27	0.1	3	0.1	
Maximum value				81	9207	29.7	1974	14.2	

[a]Refers to Fig. 1.
[b]Represents the estimated bankfull discharge for a 2-yr return interval.
[c]Expresses the conformity of the ranked annual peak flows to a ln-normal distribution used to generate "bankfull discharge" (see text). See text and T variables.

Flood[b] ($m^3 s^{-1}$)	r^2[c]	PREDQ	C/P	ANNCV	FLODFREQ (yr^{-1})	FLODINT (d)	FLODDUR (d)	FLOD60D (fraction in 60d)	FLODFREE (number of 365 d)	FLODTIME (day of water year)
98.0	.99	.38	.49	41.7	.75	284	1.5	.61	101	155
132.3	.96	.53	.67	28.9	.71	397	1.4	.50	165	138
256.0	.98	.34	.45	45.9	.71	417	1.2	.52	169	172
65.7	.98	.33	.55	40.0	1.00	166	1.3	.36	72	162
20.2	.94	.27	.98	25.3	.75	189	2.1	.60	190	121
15.9	.98	.30	.47	128.9	1.29	29	2.5	.48	154	122
7.9	.96	.18	.21	85.7	1.25	37	2.0	.69	210	139
24.9	.99	.62	.68	22.8	.91	328	11.1	.78	155	235
2.2	.99	.43	.55	40.4	.97	203	10.1	.68	137	216
63.1	.91	.61	.72	23.8	1.25	53	2.0	.59	183	120
104.1	.93	.63	.66	22.4	.83	114	2.1	.50	142	120
93.3	.97	.32	.33	57.5	1.21	51	2.1	.68	222	126
80.3	.97	.22	.18	79.8	1.19	57	2.1	.64	223	131
58.3	.97	.80	.88	21.3	.70	355	12.5	.98	296	246
13.5	.93	.66	.45	37.5	.77	339	10.9	1.00	331	254
23.2	.99	.58	.46	35.7	.73	362	8.5	.86	230	254
160.0	.96	.71	.87	12.0	.88	368	1.6	.36	73	288
213.8	.98	.43	.83	25.1	1.02	176	4.8	.51	58	160
71.2	.98	.43	.82	23.8	.98	158	2.8	.40	142	233
58.9	.94	.31	.11	76.2	1.14	116	2.4	.39	109	202
71.2	.96	.38	.51	43.3	.78	465	1.0	.57	89	181
133.6	.96	.35	.59	38.5	1.10	147	2.2	.50	130	180
68.4	.96	.37	.58	39.4	.70	364	1.1	.37	117	164
8.6	.98	.33	.79	26.6	1.07	76	2.8	.40	152	252
15.7	.98	.16	.31	89.5	1.11	61	3.0	.57	153	271
187.7	.99	.35	.52	42.9	.71	265	1.1	.46	95	159
173.3	.96	.44	.68	30.6	.67	395	1.2	.42	65	150
89.6	.93	.36	.58	38.7	.66	275	1.8	.50	111	128
161.6	.97	.60	.77	20.6	.59	383	4.1	.84	234	210
3.3	.70	.76	.92	8.7	.48	336	2.6	.50	176	217
58.9	.92	.50	.64	29.9	.82	356	2.3	.61	166	211
220.3	.97	.21	.43	56.2	.81	227	1.8	.50	55	19
294.4	.96	.35	.57	42.7	.76	232	1.3	.45	187	159
44.5	.94	.75	.71	19.4	.79	342	4.4	.87	200	227
23.7	.94	.76	.67	22.3	.67	361	8.3	.97	238	242
78.7	.98	.76	.89	10.3	.63	373	1.2	.44	109	163
79.4	.98	.69	.91	11.0	.74	375	1.1	.36	63	165
53.3	.98	.40	.59	37.5	.85	246	3.5	.30	48	169
3.4	.90	.52	.69	186.3	.92	318	14.4	.83	216	192
7.2	.60	.79	.96	1.2	.85	191	1.6	.39	127	222
95.2	.96	.62	.90	14.8	1.14	179	1.4	.52	197	249
19.2	.96	.35	.79	195.4	.75	285	1.4	.53	207	297
4.2	.98	.31	.71	36.2	.75	226	7.3	.46	126	285
36.1	.97	.63	.88	14.6	1.05	125	3.0	.40	31	141
13.3	.98	.63	.72	20.6	.77	198	11.0	.80	199	233
6.9	.88	.36	.40	119.2	.94	320	5.4	.71	143	18
6.4	.99	.23	.99	33.5	1.09	54	5.6	.48	207	165
118.5	.97	.53	.70	27.2	.71	290	1.3	.62	78	169
141.9	.96	.50	.66	29.3	.63	368	1.4	.53	90	147
131.0	.96	.46	.73	30.0	.84	341	1.8	.47	156	162
201.5	.97	.44	.85	24.3	.82	245	1.5	.46	79	195
45.0	.87	.41	.68	35.8	1.05	185	1.2	.57	176	246
32.0	.98	.20	.36	121.2	1.00	176	1.3	.61	61	234
12.7	.95	.82	.83	10.3	.82	325	1.9	.70	250	105
22.5	.89	.52	.55	34.0	.84	334	1.5	.67	221	83
37.9	.89	.79	.90	7.1	.68	355	3.8	.61	141	110
31.1	.93	.46	.51	35.4	.88	307	13.6	.75	214	179
119.7	.97	.63	.81	17.5	.84	247	1.7	.43	61	162
152.2	.99	.45	.69	29.7	.72	311	1.2	.49	27	163
8.0	.95	.73	.97	4.2	.56	658	1.1	.50	129	119
82.7	.98	.24	.30	68.3	.85	75	4.0	.44	202	202
17.0	.99	.53	.76	22.6	.79	277	4.1	.51	141	187
127.1	.98	.55	.72	24.5	.60	397	1.2	.55	142	122
160.0	.96	.65	.96	10.8	.91	181	1.6	.52	65	217
30.7	.97	.20	.24	68.3	.75	351	1.1	.50	73	216
50.1	.95	.26	.59	169.2	.80	270	1.8	.50	84	224
17.6	.96	.18	.29	111.7	.95	306	1.6	.40	203	272
2.0	.91	.67	.85	13.0	.75	65	17.7	.69	155	182
1.4	.93	.25	.45	51.0	.86	350	5.0	.88	225	225
54.9	.97	.53	.80	21.5	.67	333	1.4	.35	53	184
47.2	.97	.55	.73	24.5	.62	383	2.0	.70	119	201
14.2	.99	.80	.88	8.2	.57	449	5.6	.58	167	95
12.1	.96	.70	.74	18.1	.78	344	2.3	.64	259	105
99.0	.97	.66	.74	18.7	.58	379	1.5	.74	256	82
7.4	.94	.69	.95	9.6	.74	367	1.2	.57	123	175
122.1	.99	.48	.76	26.7	.70	401	1.1	.39	43	156
92.3	.96	.83	.68	20.8	.59	376	4.1	1.00	332	260
31.3	.95	.52	.48	42.0	.65	366	4.9	1.00	319	250
		.49	.66	41.6	.83	271	3.5	.58	152	
		.16	.11	1.2	.48	29	1.0	.30	27	
		.83	.99	195.4	1.29	658	17.7	1.00	332	

ee text and Table 1 for explanation of other

Estimation of Size-Specific Molting Probabilities in Adult Decapod Crustaceans Based on Postmolt Indicator Data

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For crustaceans that exhibit a well-defined molting season, postmolt indicator methods may be used to classify a sample of animals collected after the molting season into those that have molted and those that have failed to molt. This binary classification of a sample may be used to estimate size-specific molting probabilities. We derive maximum likelihood estimators for these molting probabilities, and for the variances of estimated molting probabilities, based on such postmolt indicator data. Estimators assume that the premolt–postmolt relation is linear with an additive and normally distributed error term of constant variance and, in their simplest form, assume that the ratio (R_i) of size-specific survival probabilities through the molting season for molting as compared with nonmolting individuals is known. For the more likely situation in which only a plausible range for R_i is specifiable, an estimation procedure is proposed which minimizes the maximum possible error (mean square error) of the molting probability estimator over this range. We illustrate application of estimators using shell condition data collected from the northern California population of adult female Dungeness crabs (*Cancer magister*). Estimated annual molting probabilities for adult female Dungeness crabs were greater than 0.90 for crabs less than 135 mm carapace width, but then declined rapidly until they were near zero for crabs exceeding 160 mm carapace width. This conclusion was not substantively affected by choices of a survival ratio ranging from 0.4 to 1.0.

Certains crustacés muent durant une période bien définie, ce qui permet d'utiliser des indicateurs caractéristiques de la période suivant la mue pour classer les échantillons recueillis après la période de meu selon que les animaux ont mué ou non. Cette classification peut servir à l'estimation des probabilités de mue en fonction de la taille. Des données portant sur les indicateurs caractéristiques de la période suivant la mue nous servent à déterminer des estimateurs de vraisemblance maximale relatifs à ces probabilités de mue et aux variances des probabilités estimées. Avec ces estimateurs, on suppose que la relation entre les périodes précédant et suivant la mue est linéaire et comporte un terme d'erreur additif à distribution normale et à variance constante; en outre, lorsque l'on utilise les estimateurs sous leur forme la plus simple, on suppose comme connu le rapport (R_i) des probabilités de survie en fonction de la taille pendant la période de la mue pour les sujets qui muent et les sujets qui ne muent pas. Pour ce qui est de la situation plus vraisemblable où l'on ne peut définir qu'une plage de R_i plausible, on propose une méthode d'estimation avec laquelle on réduit au minimum l'erreur maximale possible (erreur quadratique moyenne) liée à l'estimateur des probabilités de mue entre ces limites. Pour illustrer l'application des estimateurs, nous nous servons de données recueillies sur l'état de la carapace d'une population de crabes (*Cancer magister*) femelles adultes du nord de la California. La valeur estimative des probabilités de mue annuelle chez ces crabes s'est révélée supérieure à 0,90 pour ceux dont la carapace mesurait moins de 135 mm de largeur, mais elle baissait rapidement jusqu'à une valeur presque nuelle pour ceux dont la carapace dépassait 160 mm de largeur. Le fait qu'on ait utilisé un rapport de survie se situant entre 0,4 et 1,0 n'a pas vraiment influé sur ce résultat.

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Estimates of size-specific molt increments and molting probabilities, when combined with estimates of intermolt intervals, have provided the basis for quantitative description of a crustacean's growth pattern (e.g. Weber and Miyahara 1962; Hancock and Edwards 1967; Bennett 1974; McCaughran and Powell 1977; Campbell 1983). Size-specific molt increments have often been found to be a two-phase (juvenile–adult) linear function of premolt size (Butler 1961; Kurata 1962), and estimation of the parameters of this function has posed few substantive problems (Hinkley 1971; Seber 1977; Somerton 1980). In contrast, estimation of size-specific molting probabilities has proved difficult, for reasons detailed below. Steep, nonlinear declines in molting probabilities with increasing premolt size have nevertheless been documented for several commercially important crustaceans (Weber and Miyahara 1962 — king crab; Bennett 1974 — European edible crab; Campbell 1983 — American lobster; Hankin et al. 1989 — Dungeness crab) and illustrate the importance of accurately assessing size-dependence of molting probabilities.

Estimation of molting probabilities in adult decapod crustaceans has traditionally been based on data generated from mark–recapture experiments (e.g. Hancock and Edwards 1967). Marked samples need not be representative of population size structure, and recapture samples need only be random with respect to whether or not an individual was or was not destined

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to molt during its time at large. Molt increment data are obtained through the recovery process, thus allowing concurrent description of the size-dependence of molt increments, and the approach may be used for species that do not exhibit a well-defined molting season(s).

The mark–recapture approach is not without shortcomings, however. Size frequencies of commercial fishery recoveries will depend on the size-selective properties of commercial recovery gear. Recoveries obtained from stationary traps, in particular, may be seriously biased toward larger and/or molted animals (Diamond and Hankin 1985). Mark–recapture studies designed to allow estimation of molting probabilities have either ignored trap selection bias (Conan and Gunderson 1979; McCaughran and Powell 1977), or have restricted attention to animals that were fully vulnerable to the commercial recovery gear (Hancock and Edwards 1967; Campbell 1983). In addition, the assumption that recoveries of molted and nonmolted animals are random with respect to molting history invokes an implicit assumption that survival rates through the molting season are equal for molted and nonmolted animals.

An alternative, and less costly, approach for estimation of molting probabilities may exist for species that exhibit a well-defined molting season. Based on physical appearance (external or histological) or chemical composition, one may accurately classify a sample of animals collected just prior to (or just after) a molting season into (1) those that will molt during the upcoming season (or have molted), and (2) those that will not molt during the upcoming molting season (or have not molted). This binary classification of a sample can be used for estimation of molting probabilities. Promising premolt indicators include integumental structure (Hepper 1965; Aiken 1980), serum protein concentration (Ennis 1973; Stewart and Li 1969) and pleopod regenerative state (Aiken 1973, 1980). External carapace condition (shell condition) (Weber and Miyahara 1962; Ennis 1977) and serum protein concentration (Ennis 1977) have been used as postmolt indicators. The duration of a molting season may often exceed the "notification time" of a premolt indicator however, or classification of animals based on a premolt indicator may be unreliable, time-consuming or expensive. In such cases, postmolt indicators may prove more practical for estimation of size-specific molting probabilities.

Estimation of molting probabilities based on a molt/nonmolt classified postseason sample (exemplified in parts A and B of Fig. 1) consists of reconstructing this sample's size frequency distribution as it existed prior to the molting season, and classifying the numbers of animals within each size interval according to whether or not they were destined to molt during the molting season. There are two basic steps involved in reconstruction of the preseason size frequency distribution. First, for molted animals, one must predict their corresponding premolt size interval(s). (Nonmolted animals remained in their respective preseason size intervals.) It is simplest to assume that molt increments are independent of premolt size and are of fixed magnitude Δ. The premolt size distribution for molted animals can then be obtained simply by shifting their postmolt size distribution to the left by the amount Δ (part C of Fig. 1). Second, one must account for the possibility that survival rates through the molting season may have differed between animals that molted and animals that did not molt. If survival rates for animals that molted are less than for those that did not molt, then the premolt size frequency distribution for molted animals must be adjusted upwards relative to the size frequency distribution of nonmolted animals. If one assumes that survival rates through the molting season are independent of preseason size and are the same for molting and nonmolting animals, then no adjustments are necessary. Part D of Fig. 1 illustrates the results of a preseason size frequency reconstruction using these simplest possible assumptions (constant molt increment and equal survival rates through the molting season, as assumed by Weber and Miyahara (1962) in their analyses of king crab data). Estimates of size-specific molting probabilities are then calculated as the proportions of animals destined to molt within any given size interval.

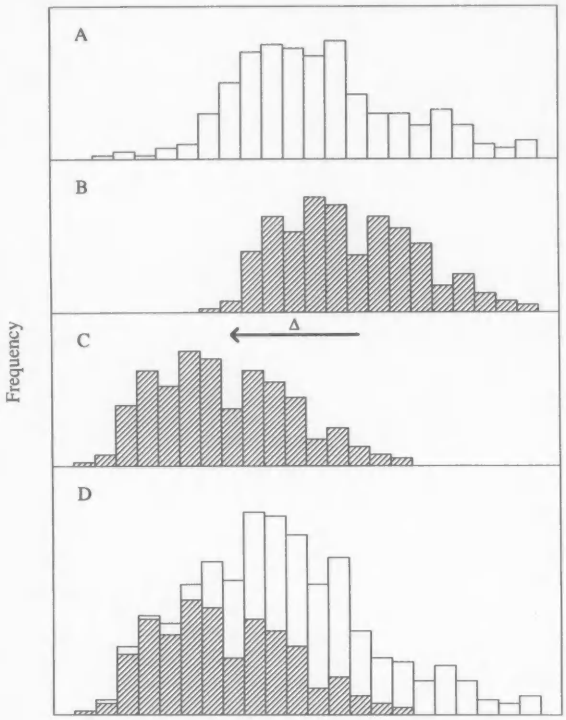

FIG. 1. Graphical illustration of the problem of estimation of size-specific molting probabilities from postseason molt indicator data. Parts A and B indicate the postseason size frequencies of nonmolted and molted animals, respectively (fictitious data). Part C indicates the preseason size frequencies of the (part B) molted animals, obtained from part B using a constant molt increment (shift factor, Δ). If survival rates through the molting season are assumed equal for molting and nonmolting animals, then the summation of the frequency distributions in part A and C, as shown in part D, can be used to obtain estimates of size-specific molting probabilities as the proportions of animals destined to molt within any given size interval. Shaded portions show animals that molted or were destined to molt.

In this paper we present a more realistic approach to reconstruction of the preseason size frequency distribution and estimation of size-specific molting probabilities, based on classification of a sample collected after a molting season into molted and nonmolted groups. Classification relies, in general, on an unspecified postmolt indicator. We allow molt increments to depend on premolt size and exhibit natural variation, and we also account for the possibility that survival rates through the molting season may vary between molting and nonmolting ani-

mals. Perhaps the most important feature of our work, however, is that models and assumptions are explicitly formulated which in turn allows for the derivation of sampling variance formulas for calculated estimates of molting probabilities. Application of methods is illustrated using shell condition data collected from the northern California population of adult female Dungeness crabs (*Cancer magister*) (Hankin et al. 1989). Methods we develop and illustrate should be applicable to other crustaceans that exhibit a well-defined molting season and for which a reliable postmolt indicator exists.

Estimators

In this section we present simplified derivations of estimators of size-specific molting probabilities and associated sampling variances. Complete formal derivations of estimators, including assessments of their asymptotic properties, are presented in Appendix A.

Let $x_i - \frac{1}{2}h < X \leq x_i + \frac{1}{2}h$ represent the ith size interval, with midpoint x_i, for which estimates of molting probability are desired (e.g. $h = 3.0$ mm). Denote by $P_{pre,i}$ the probability that an individual belonged to (preseason) size interval i and molted given that it survived through the molting season, and by $S_{i,m}$ the probability of such survival for a molted individual. Similarly, define by $P_{fail,i}$ the probability that an individual belonged to (preseason) size interval i and failed to molt given that it survived through the molting season, and by $S_{i,f}$ the probability of such survival for a nonmolted individual. (Note that a nonmolting individual in size interval i will remain in that size interval if it survives the molting season.) The probability of molting from the ith size interval, P_i, may thus be expressed as

$$(1)\quad P_i = \frac{P_{pre,i}/S_{i,m}}{(P_{pre,i}/S_{i,m}) + (P_{fail,i}/S_{i,f})} = \frac{P_{pre,i}}{P_{pre,i} + R_i P_{fail,i}},$$

where $R_i = S_{i,m}/S_{i,f}$ (the ratio of survival probabilities through the molting season for molting as compared with nonmolting individuals).

Now consider a partitioning of the molted animals' postseason size range as consisting of intervals $y_j - \frac{1}{2}g < Y \leq y_j + \frac{1}{2}g$, with midpoint y_j, where the interval width g depends principally on the accuracy with which the animals can be measured (e.g. $g = 0.1$ mm with the recorded sizes of all postmolt individuals equal to some midpoint y_j). Let $P_{post,j}$ represent the probability that an individual has molted and belongs to this postmolt size interval given that it survived through the molting season. Define π_{ij} as the probability that an individual belonged to preseason size interval i given that it molted to postmolt size y_j and survived through the molting season. Then, $\pi_{ij} P_{post,j}$ is the probability that an individual molted from premolt size interval i to postmolt size y_j given that it survived through the molting season so that $P_{pre,i} = \sum_j \pi_{ij} P_{post,j}$ and

$$(2)\quad P_i = \frac{\sum_j \pi_{ij} P_{post,j}}{\sum_j \pi_{ij} P_{post,j} + R_i P_{fail,i}},$$

where the summations extend over all possible postmolt sizes y_j for the premolt size interval i.

R_i Known

Equation (2) provides the basis for estimation of P_i using observable quantities. From a postseason molt composition random sample of size n_1, the maximum likelihood estimates for multinomial probabilities $P_{post,j}$ and $P_{fail,i}$ are the sample proportions:

$$(3)\quad \hat{P}_{post,j} = n_{post,j}/n_1, \qquad \hat{P}_{fail,i} = n_{fail,i}/n_1;$$

where $n_{post,j}$ are the number of individuals classified as having molted and of (postmolt) size $y_j \pm \frac{1}{2}g$; $n_{fail,i}$ are the number of individuals classified as having failed to molt and of size $x_i \pm \frac{1}{2}h$; and $n_1 = \sum_j n_{post,j} + \sum_i n_{fail,i}$.

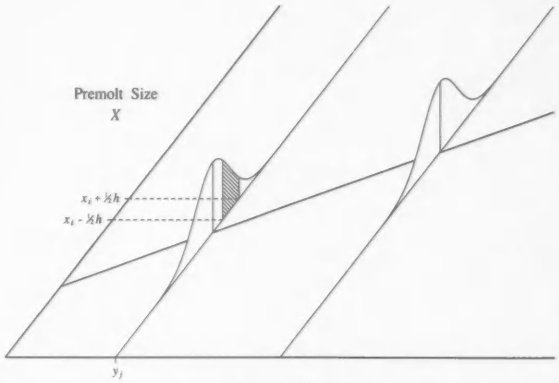

FIG. 2. Graphical illustration of the assumed premolt–postmolt stochastic model: $X = \alpha + \beta Y + \epsilon$; $\epsilon \sim N(0,\sigma^2)$. The additive and normally distributed error term of constant variance reflects natural variation of size-specific molt increments. The shaded area under the curve is equal to the conditional probability (π_{ij}) of having molted from the premolt size interval $x_i - \frac{1}{2}h < X \leq x_i + \frac{1}{2}h$ given an observed postmolt size of $Y = y_j$.

Estimation of the π_{ij} requires specification of the premolt–postmolt relationship. We assume that premolt size (X) is a linear function of postmolt size (Y) with an additive and normally distributed error term (ϵ) of constant variance (σ^2):

$$(4)\quad X = \alpha + \beta Y + \epsilon; \qquad \epsilon \sim N(0,\sigma^2).$$

For this case, π_{ij} is illustrated graphically in Fig. 2 and defined analytically as

$$(5)\quad \pi_{ij} = \Phi(\bar{z}_{ij}) - \Phi(\underline{z}_{ij}) \text{ with}$$

$$(6)\quad \bar{z}_{ij} = \frac{(x_i + \frac{1}{2}h) - (\alpha + \beta y_j)}{\sigma};$$

$$\underline{z}_{ij} = \frac{(x_i - \frac{1}{2}h) - (\alpha + \beta y_j)}{\sigma}$$

where $\Phi(\cdot)$ denotes the standard normal cumulative distribution function. Maximum likelihood estimates of the π_{ij} are obtained by substituting the maximum likelihood estimates of α, β, and σ^2 (based on n_2 independent premolt–postmolt observations) into equations (5) and (6):

$$(7)\quad \hat{\alpha} = \bar{x} - \hat{\beta}\bar{y}; \quad \hat{\beta} = \frac{\sum (x_i - \bar{x})(y_i - \bar{y})}{\sum (y_i - \bar{y})^2};$$

$$\hat{\sigma}^2 = \frac{\sum (x_i - (\hat{\alpha} + \hat{\beta} y_i))^2}{n_2}.$$

The maximum likelihood estimator of P_i is then given by substitution of estimated π_{ij}, $P_{post,j}$, $P_{fail,i}$ into equation (2). The

resulting estimator is, in the statistical sense, consistent and asymptotically efficient so that, at least for large samples, $\hat{P}_i$ is making the best possible use of the available information (Appendix A). For large n_1, n_2, $\hat{P}_i$ is approximately normally distributed with expectation P_i and variance given by

$$(8)\quad V(\hat{P}_i) = \left(\frac{P_i}{P_{pre,i}}\right)^2 \left(C_{mult,i} + \frac{(1-P_i)^2}{\sigma^2} C_{reg,i}\right),$$

where $C_{mult,i}$ results from uncertainty associated with the molt composition (multinomial) sample and $C_{reg,i}$ results from uncertainty associated with the premolt–postmolt (regression) relationship. $C_{mult,i}$ and $C_{reg,i}$ are of complicated form and are derived in Appendix A (equations (A17) and (A22)). An estimator for $V(\hat{P}_i)$ is obtained by substitution of appropriate maximum likelihood estimates into equation (8).

R_i Unknown

In the usual case, the ratio of size-specific survival probabilities through the molting season for molting as compared with nonmolting animals, R_i, will be unknown. (In Appendix B we provide an estimator for R_i based on comparison of preseason and postseason indicator data, but a direct (preseason) estimate of P_i would be possible if valid preseason data were available.) Although the estimator we have proposed for P_i, based on postseason indicator data, explicitly allows for $R_i \neq 1$, of what use is this estimator if a precise estimate of R_i is not available? When R_i is unknown, one may examine the sensitivity of the estimator $\hat{P}_i$ to values of R_i taken over a plausible range (say, $0.5 < R_i \leq 1.0$). If resulting estimates are relatively insensitive to such values of R_i, the bias introduced into $\hat{P}_i$ from use of any particular choice of R_i will be relatively small.

We therefore outline a second approach which makes full use of a plausible interval for R_i and we formulate corresponding errors of estimation in this more realistic setting. We begin by noting the way in which substitution of an (arbitrary) value, R_i^*, for R_i influences the variance and, more importantly, the bias of the P_i estimator. For a given value R_i^*, all results presented above for the case of R_i known hold with R_i^* in place of R_i: the estimator $\hat{P}_i^*$ (equation (2) with R_i^*, $\hat{\pi}_{ij}$, $\hat{P}_{post,j}$, and $\hat{P}_{fail,i}$ replacing R_i, π_{ij}, $P_{post,j}$, and $P_{fail,i}$) is asymptotically normally distributed with expectation P_i^* (equation (2) with R_i^* replacing R_i) and variance as in equation (8) (with P_i^* and R_i^* replacing P_i and R_i), and $\hat{P}_i^*$ is consistent and asymptotically efficient for P_i^*. In considering $\hat{P}_i^*$ as an estimator for P_i, however, variance is no longer an adequate measure of uncertainty because $\hat{P}_i^*$ is biased with respect to the true P_i. The asymptotic bias of $\hat{P}_i^*$ for P_i is given by $B(\hat{P}_i^*) = P_i^* - P_i$ (Appendix A):

$$(9)\quad B(\hat{P}_i^*) = P_i^* \left(1 - \frac{1}{P_i^* + \frac{R_i}{R_i^*}(1-P_i^*)}\right).$$

Notice that $B(\hat{P}_i^*)$ depends on the ratio R_i/R_i^*; if $(R_i/R_i^*) = 1$, then $B(\hat{P}_i^*) = 0$.

An appropriate measure for the accuracy of $\hat{P}_i^*$ as an estimator of P_i is therefore mean square error (which includes contributions of both sampling variance and bias). The asymptotic mean square error of $\hat{P}_i^*$ is given by

$$(10)\quad MSE(\hat{P}_i^*) = B^2(\hat{P}_i^*) + V(\hat{P}_i^*).$$

Thus, for given R_i, R_i^* and large n_1, n_2, a close approximation to $MSE(\hat{P}_i^*)$ may be obtained by substitution of the appropriate maximum likelihood estimates into equations (8) (with P_i^* and R_i^* replacing P_i and R_i) and (9) and applying relation (10).

We thus propose the following general estimation procedure. For each size interval i, specify a plausible range for R_i. Denote the lower and upper bounds of this range by $R_{l,i}$ and $R_{u,i}$, respectively. For a given R_i^*, determine the maximum value taken on by $M\hat{S}E(\hat{P}_i^*)$ over the full plausible range of R_i: $\max M\hat{S}E(\hat{P}_i^*)$. Select for $R_{opt,i}^*$ that value of R_i^* ($R_{l,i} \leq R_i^* \leq R_{u,i}$) that minimizes $\max M\hat{S}E(\hat{P}_i^*)$. That is, select $R_{opt,i}^*$ such that

$$(11)\quad \max_{R_{l,i} \leq R_i \leq R_{u,i}} [M\hat{S}E\,(\hat{P}_i^*)]$$

is minimized. This minimax criterion will protect against large errors of estimation that may result from a particular choice of R_i^* when the true R_i is unknown.

Calculations of the proposed procedure are simplified considerably by noting the following. For given R_i^*, $\hat{V}(\hat{P}_i^*)$ does not depend on R_i. Also, for given R_i^*, $\hat{B}^2(\hat{P}_i^*)$ is a concave function of R_i ($\partial \hat{B}^2(\hat{P}_i^*)/\partial R_i \gtrless 0$ for $R_i \gtrless R_i^*$) and is maximized over the interval $R_{l,i} \leq R_i \leq R_{u,i}$ at either $R_i = R_{l,i}$ or $R_i = R_{u,i}$. Thus, equation (11) becomes:

$$(12)\quad \hat{V}(\hat{P}_i^*) + \max[\hat{B}^2(\hat{P}_i^* | R_i = R_{l,i}),\ \hat{B}^2(\hat{P}_i^* | R_i = R_{u,i})]$$

which can be directly calculated given a particular R_i^*.

It may be that on the basis of the $R_{opt,i}^*$ calculations, and with no biological evidence to the contrary, a single, size-independent, optimal choice, R_{opt}^*, is desired. In this case, the criterion of equation (11) may be extended to provide the value R_{opt}^* that gives the best overall protection concerning all the P_i estimates ($i = 1,2,\ldots,I$). For a specified R interval, select that value R^* such that the sum total of the maximum possible errors is minimized. That is, select R_{opt}^* such that

$$(13)\quad T(R^*) = \sum_{i=1}^{I} \max_{R_l \leq R \leq R_u} [M\hat{S}E(\hat{P}_i^*)]$$

is minimized.

For either case (R_i^* or R^*) approximate 95% confidence intervals for P_i can be formed as $\hat{P}_i^* \pm 2\sqrt{\max M\hat{S}E(\hat{P}_i^*)}$. Hansen et al. (1953, p. 58, table 1) show that such intervals will in general be conservative (i.e. at least 95% coverage probability).

Application: Adult Female Dungeness Crabs (*Cancer magister*)

Estimators presented in the previous section were originally developed for application to the northern California population of female Dungeness crabs. Adult female Dungeness crabs are known to exhibit a well-defined and relatively short annual molting season during which individuals undergo, at most, a single molt (Butler 1961; Wild 1980; Hankin et al. 1989). In northern California, the molting season is approximately 6–8 wk long and usually extends from early April through mid-May (Hankin et al. 1989). Application of these estimators is illustrated below using shell condition data reported in Hankin et al. (1989).

Actual calculations, described below, were carried out on a VAX 11/780 computer using a FORTRAN program written by the senior author. Because application of our proposed methods would in general require that similar programs be constructed by other investigators, we have developed a version of this program for distribution. Copies of the FORTRAN program source code, an accompanying "user's guide", and example appli-

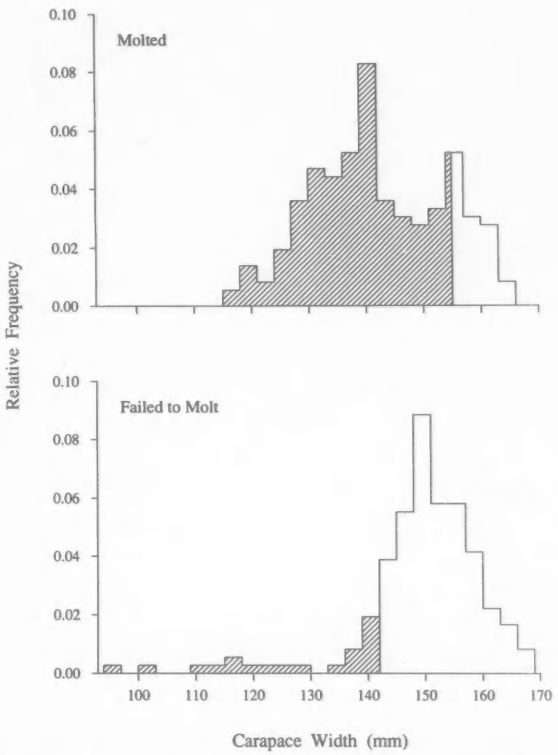

FIG. 3. Relative frequencies (per 3.0-mm interval) of postmolting season carapace widths among crabs that were classified as having molted or as having failed to molt ($n_1 = 362$). Shaded regions indicate crabs that probably molted from premolt carapace widths less than 142 mm (molted group), or that failed to molt from carapace widths less than 142 mm (failed to molt group).

cations based on the data reported in this paper, may be obtained from the second author.

Molt Composition

Samples of adult female crabs were collected following the 1983 molting season using stationary trap gear known to be nonselective over the adult size range, about 90 to 170 mm carapace width (see Diamond 1983; and Diamond and Hankin 1985, for details of sampling methods, trap design, and trap size-selection characteristics). Sampling was conducted shortly after the molting season, in late May, and crabs could be assigned to molting category (molted or failed to molt) with near certainty. Classification was based primarily on coloration of the ventral exoskeleton. Fresh exoskeletons were bright in appearance and undersides were white and devoid of discoloration or fouling. In contrast, undersides of aged exoskeletons were darker, joints of walking appendages were usually blackened, and exoskeletons were often heavily fouled (see also Butler 1961).

Size frequency histograms of crabs ($n_1 = 362$) classified into molted and nonmolted groups (Fig. 3) suggested strong size dependence of molting probabilities. Only 15% (24/161) of those crabs that failed to molt were less than 142 mm carapace width. Hankin et al. (1989) found that molt increments averaged about 13 mm for crabs of 142 mm premolt carapace width.

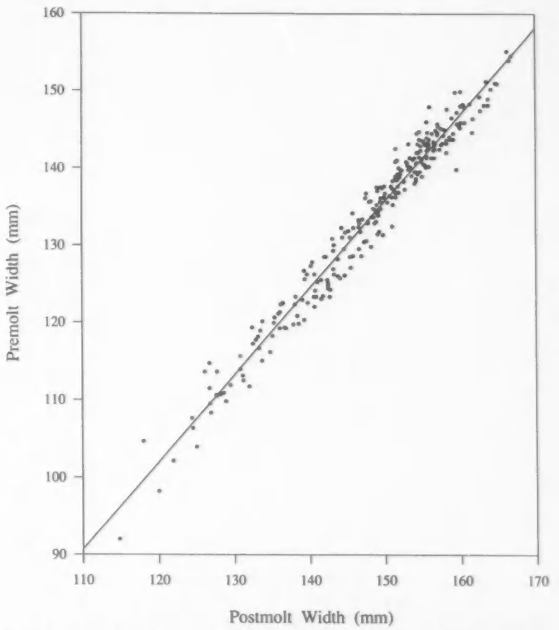

FIG. 4. Premolt carapace width (X) plotted against postmolt carapace width (Y) based on data reported in Hankin et al. (1989) for adult female Dungeness crabs in northern California. Solid line depicts the fitted relation $\hat{X} = -32.8484 + 1.1234Y$, as estimated from these data ($n_2 = 277$).

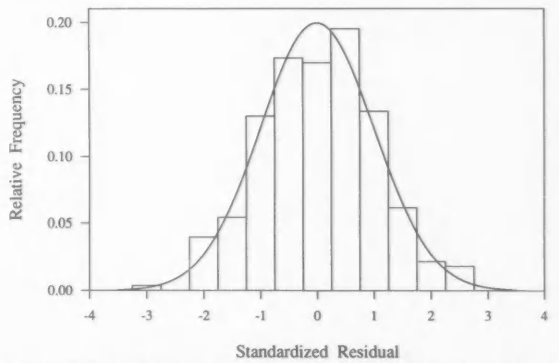

FIG. 5. Relative frequency (per one-half standard unit interval) of grouped, unconditional, standardized residuals (Draper and Smith 1981, p. 144) derived from the data presented in Fig. 4. Curved line depicts an appropriately scaled standard normal density.

Therefore, molted crabs with carapace widths less than 155 mm had probably molted from premolt sizes less than 142 mm. Crabs with carapace widths less than 155 mm accounted for about 82% (165/201) of all crabs that had molted. The steep decline in numbers of molted crabs beyond 155 mm carapace width, when contrasted with the high frequency of crabs this size or larger among nonmolted crabs, suggested that molting probabilities must be low among large adult female Dungeness crabs.

Premolt–Postmolt Relation

Estimation of the premolt–postmolt relation was based on $n_2 = 277$ independent (single) molt increments generated from

TABLE 1. Postseason molt composition sample of size $n_1 = 362$ grouped over $h = 3.0$-mm intervals. Carapace width indicates interval midpoint. Column $\mathbf{n}_{post}$ gives the observed postmolt size (width) frequency distribution while $\hat{\mathbf{n}}_{pre}$ (see equation (15)) gives the estimated premolt size (width) frequency distribution of these individuals. Column $\mathbf{n}_{fail}$ gives the observed size (width) frequency distribution of those individuals which failed to molt.

Carapace width (mm)	$\mathbf{n}_{post}$	$\hat{\mathbf{n}}_{pre}$	$\mathbf{n}_{fail}$
92.5	0	0.03	0
95.5	0	0.49	1
98.5	0	2.04	0
101.5	0	3.26	1
104.5	0	3.64	0
107.5	0	6.38	0
110.5	0	10.29	1
113.5	0	12.66	1
116.5	2	14.63	2
119.5	5	15.70	1
122.5	3	20.53	1
125.5	7	21.09	1
128.5	13	14.23	1
131.5	17	9.69	0
134.5	16	9.00	1
137.5	19	10.37	3
140.5	30	13.92	7
143.5	13	14.35	14
146.5	11	9.60	20
149.5	10	5.91	32
152.5	12	2.60	21
155.5	19	0.56	21
158.5	11	0.03	15
161.5	10	0.00	8
164.5	3	0.00	6
167.5	0	0.00	3
Total	201	201.00	161

both mark–recapture and laboratory molting of crabs (see Hankin et al. 1989 for details on collection of molt increment data and for comparison of molt increments from the two sources). The fitted linear relation, using the maximum likelihood estimators given by equation (7), was (Fig. 4)

$$(14)\quad \hat{X} = -32.8484 + 1.1234\,Y,$$

where $\hat{X}$ is predicted premolt carapace width (in millimetres, excluding tenth anterolateral spines), and Y is postmolt carapace width. Linearity, over the size range examined, was evident (Fig. 4) as well as an additive error term of constant variance ($\hat{\sigma}^2 = 4.1051$). A standard normal curve superimposed over a histogram of the unconditional, standardized residuals (Fig. 5) (following Draper and Smith 1981, p. 144) suggested that the assumption of a normally distributed error term was reasonable.

Estimation of Annual Molting Probabilities

Observed postmolt sizes of molted crabs were grouped using a 0.1-mm interval (i.e. $g = 0.1$, corresponding to the level of measurement accuracy). A 3.0-mm interval was used for grouping observed sizes of nonmolted crabs (i.e. $h = 3.0$). In computing the $\hat{\pi}_{ij}$ based on equations (5) and (6), we used the polynomial expression for $\Phi(\cdot)$ given by Zelen and Severo (1965, equation 26.2.17), which results in a maximum error of 1.5×10^{-7}. (A less accurate alternative would have been to use tables of "areas under the standard normal curve", e.g. Snedecor and Cochran 1980, p. 468, table A3.) Given estimates

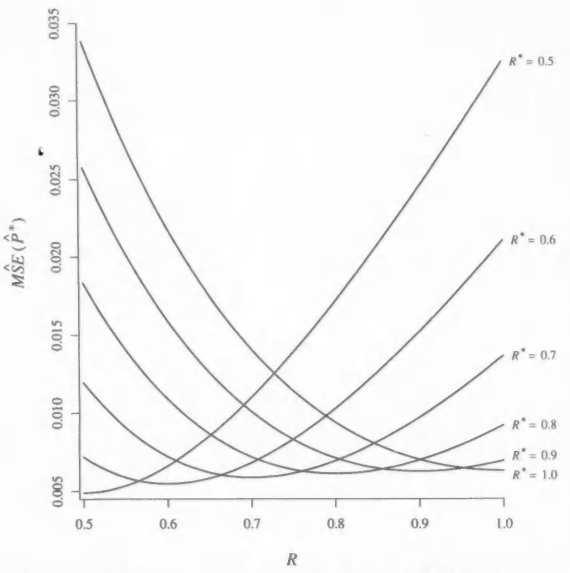

FIG. 6. Illustration of the relationship between $\hat{MSE}(\hat{P}_i^*)$, R_i^*, and R_i for a particular interval i (carapace width (midpoint), $x_i = 143.5$ mm). For the set $R^* = \{0.5, 0.6, 0.7, 0.8, 0.9, 1.0\}$ and assuming $0.5 \leq R \leq 1.0$, the maximum estimated mean square error is minimum for $R^* = 0.7$. Subscripts are omitted on figure labels.

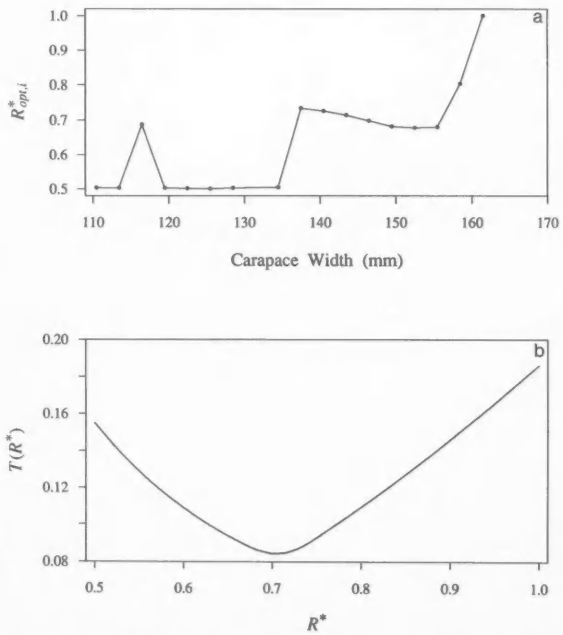

FIG. 7. (a) Size-specific optimal choice of survival ratio ($R^*_{opt,i}$), based on minimization of equation (11) under an assumption that $0.5 \leq R_i \leq 1.0$. (b) Size-independent optimal choice of survival ratio (R^*_{opt}). $T(R^*)$, defined by equation (13), is plotted as a function of R^* assuming that $0.5 \leq R \leq 1.0$. $T(R^*)$ is minimum for $R^* \approx 0.70$.

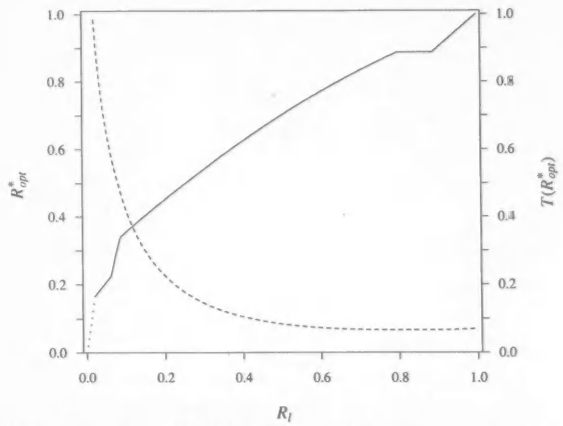

FIG. 8. Dependence of R^*_{opt} (solid line) on the lower bound, R_l, of the assumed range encompassing R: $R_l \leq R \leq 1.0$. Dashed line gives corresponding $T(R^*_{opt})$ as defined by equation (13).

of π_{ij} we then calculated $\hat{n}_{pre,i}$, the number of individuals estimated to have molted from the ith interval, using $\hat{n}_{pre,i} = \sum_j \hat{\pi}_{ij}\, n_{post,j}$.

Table 1 presents observed molt composition data ($n_{post,j}$ and $n_{fail,i}$) and $\hat{n}_{pre,i}$, all grouped by 3.0-mm intervals. For size intervals for which $\hat{n}_{pre,i} + n_{fail,i} \geq 5$, we calculated estimates of size-specific molting probabilities, based on data summarized in Table 1 and a particular choice R^*_i, using

$$(15)\quad \hat{P}^*_i = \frac{\sum_j \hat{\pi}_{ij} \hat{P}_{post,j}}{\sum_j \hat{\pi}_{ij}\, \hat{P}_{post,j} + R^*_i\, \hat{P}_{fail,i}} = \frac{\hat{n}_{pre,i}}{\hat{n}_{pre,i} + R^*_i\, n_{fail,i}}\ .$$

(We did not make estimates for intervals in which $\hat{n}_{pre,i} + n_{fail,i} < 5$ because we regarded such estimates as unreliable.)

Although R_i could not be specified precisely, a reasonable a priori assumption was that $0.5 \leq R_i \leq 1$. Before directly examining the sensitivity of the $\hat{P}^*_i$ over values of R^*_i meeting the above constraint, we illustrate the influence of R^*_i on $\hat{MSE}(\hat{P}^*_i)$ following the methods presented for R_i unknown. Figure 6 exemplifies this relationship for carapace width (midpoint) 143.5 mm under an assumption that $0.5 \leq R \leq 1.0$. In reference to Fig. 6, for $R^* = R$ the estimator $\hat{P}^*_i$ is asymptotically unbiased for P_i and, accordingly, $\hat{MSE}(\hat{P}^*_i) = \hat{V}(\hat{P}^*_i)$. However, for a given value R^*, if $R \neq R^*$ the estimator incurs bias and $\hat{MSE}(\hat{P}^*_i)$ increases accordingly. If maximum risk for a given R^* is defined as the maximum possible value taken on by $\hat{MSE}(\hat{P}^*_i)$ over the range for R, then for carapace width 143.5 mm, assuming $0.5 \leq R \leq 1.0$, the maximum risk is minimized over the considered set $R^* = \{0.5, 0.6, 0.7, 0.8, 0.9, 1.0\}$ by taking $R^* = 0.7$. That is, $R^* = 0.7$ satisfies the minimax criterion proposed for selection of $R^*_{opt,i}$ based on equation (11).

Assuming $0.5 \leq R_i \leq 1.0$, size specific $R^*_{opt,i}$ were determined and are plotted against carapace width in Fig. 7a. Recalling the example of Fig. 6, for carapace width (midpoint) 143.5 mm, we found (more accurately) $R^*_{opt} = 0.71$. Not all size intervals are represented in Fig. 7a. For those widths (midpoints) not represented (107.5, 131.5, 164.5), the estimated P_i was identically either 1 or 0 in which case $\hat{MSE}(\hat{P}^*_i)$ degenerates to 0 regardless of R^*_i. The fact that, for these size intervals, $\hat{P}^*_i$ was independent of R^*_i is important in itself and we will return to this point. Over the central portion of the adult size range (136.0 to 157.0 mm), there was notable consistency in the $R^*_{opt,i}$ (range: 0.68 to 0.73). It was also this portion of the size range where estimated molting probabilities declined rapidly from near 0.80 to near 0.05. While the $R^*_{opt,i}$ corresponding to most of the remaining size intervals were extreme (0.5 or 1.0), $\hat{MSE}(\hat{P}^*_i)$ over these intervals was only slightly effected by changes in R^*_i (due to the essential invariance of $\hat{P}^*_i$ to varying R^*_i — for these sizes). Thus, while the $R^*_{opt,i}$ values given for these size intervals did indeed minimize equation (11), other values of R^*_i in their place would have had little impact on $\hat{MSE}(\hat{P}^*_i)$ (and on $\hat{P}^*_i$).

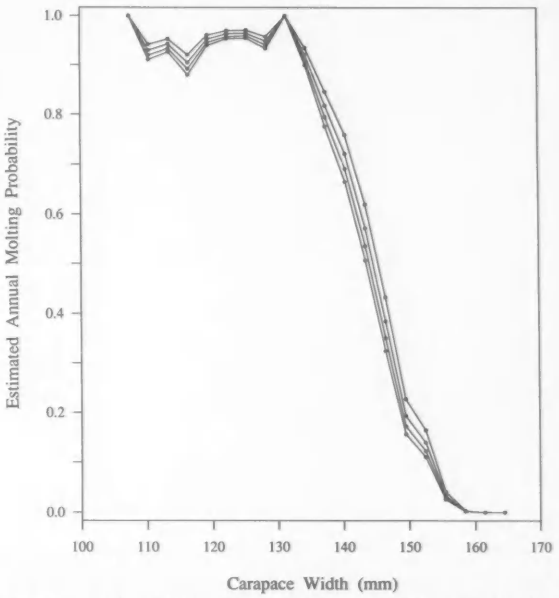

FIG. 9. Annual molting probability estimates for various values of R^*. Uppermost line is for $R^* = 0.63$ with successive lines corresponding to $R^* = 0.77$, 0.89, and 1.00, respectively. These R^* values are optimal, in the sense of minimizing $T(R^*)$ as defined by equation (13), for $R_l \leq R \leq 1.0$ with $R_l = \{0.4, 0.6, 0.8, 1.0\}$, respectively (see Fig. 8).

In view of these findings, a single size-independent survival ratio, R^*_{opt}, based on minimization of the total maximum risk, $T(R^*)$ (given by equation (13)), was considered (Fig. 7b). For $0.5 \leq R \leq 1.0$, $T(R^*)$ appeared as a concave function of R^* with minimum at $R^*_{opt} \approx 0.70$. A close correspondence between R^*_{opt} and $R^*_{opt,i}$ over the center portion of the size range was evident though not surprising in view of the relatively large $\hat{MSE}(\hat{P}^*_i)$ contributions by these sizes to $T(R^*)$. In fact, $T(R^*_{opt} = 0.70) \approx 0.084$ while the total maximum risk based on size-specific $R^*_{opt,i}$ was ≈ 0.080.

Thus far we had assumed that $R_l \leq R \leq 1.0$ with $R_l = 0.5$. Figure 8 illustrates the dependence of R^*_{opt} and $T(R^*_{opt})$ on this range for R as R_l varied from 0.02 to 1.0. In reference to Fig. 8, as R_l was decreased from 1.0 to, say, 0.4 (or even 0.2), the varying R^*_{opt} had little effect on $T(R^*_{opt})$. Thus, a conservative assumption of, say, $0.4 \leq R \leq 1.0$ would sacrifice little in so far as the total (maximal) uncertainty of the $\{\hat{P}^*_i\}$ taken as a lot is concerned.

Figure 9 illustrates $\{\hat{P}^*_i\}$ for $R^*_{opt} = \{0.63, 0.77, 0.89, 1.00\}$ corresponding, respectively, to $R_l = \{0.4, 0.6, 0.8, 1.0\}$ and an assumption that $R_l \leq R \leq 1.0$. For each R^*_{opt}, line segments con-

TABLE 2. Estimated size-specific annual molting probabilities ($\hat{P}_i^*$), their associated variances ($\hat{V}(\hat{P}_i^*)$), maximum mean square errors (max $\hat{MSE}(\hat{P}_i^*)$), and resulting confidence intervals ($\hat{P}_i^* \pm 2\sqrt{\max \hat{MSE}(\hat{P}_i^*)}$), all corresponding to $R_{opt}^* = 0.70$ and an assumption that $0.5 \leq R \leq 1.0$. Carapace width indicates midpoint of $h = 3.0$ mm grouping interval.

Carapace width (mm)	$\hat{P}_i^*$	$\hat{V}(\hat{P}_i^*)$	max $\hat{MSE}(\hat{P}_i^*)$	$\hat{P}_i^* \pm 2\sqrt{\max \hat{MSE}(\hat{P}_i^*)}$
107.5	1.000	0.00000	0.00000	1.0
110.5	0.936	0.00370	0.00432	(0.80 , 1.00)
113.5	0.948	0.00254	0.00297	(0.84 , 1.00)
116.5	0.913	0.00335	0.00443	(0.78 , 1.00)
119.5	0.957	0.00171	0.00200	(0.87 , 1.00)
122.5	0.967	0.00104	0.00122	(0.90 , 1.00)
125.5	0.968	0.00099	0.00116	(0.90 , 1.00)
128.5	0.953	0.00205	0.00240	(0.86 , 1.00)
131.5	1.000	0.00000	0.00000	1.0
134.5	0.928	0.00468	0.00545	(0.78 , 1.00)
137.5	0.832	0.00722	0.01036	(0.63 , 1.00)
140.5	0.740	0.00636	0.01187	(0.52 , 0.96)
143.5	0.594	0.00587	0.01362	(0.36 , 0.83)
146.5	0.407	0.00507	0.01196	(0.19 , 0.63)
149.5	0.209	0.00268	0.00640	(0.05 , 0.37)
152.5	0.150	0.00320	0.00552	(0.00 , 0.30)
155.5	0.037	0.00048	0.00068	(0.00 , 0.09)
158.5	0.003	0.00000	0.00001	(0.00 , 0.01)
161.5	0.000	0.00000	0.00000	0.0
164.5	0.000	0.00000	0.00000	0.0

nect the point estimates across the 3.0-mm size intervals. Estimated molting probabilities, regardless of the value of R^*, indicated a strong dependence on premolt carapace width. Point estimates of P_i were most influenced by the value of R^* for those premolt size intervals in which $0.15 < \hat{P}_i^* < 0.85$; the most extreme example being carapace width (midpoint) 143.5 where: $\hat{P}(R^* = 0.63) \approx 0.62$; $\hat{P}(R^* = 0.77) \approx 0.57$; $\hat{P}(R^* = 0.89) \approx 0.54$; $\hat{P}(R^* = 1.0) \approx 0.51$. For those size intervals in which $\hat{P}_i^*$ was either >0.85 or <0.15, the $\hat{P}_i^*$ were nearly independent of R^*. In fact, for a given size interval, if $\hat{P}_i^*$ is identically 0 or 1, correcting for differential survival in the observed numbers of molted and nonmolted animals has no effect on the estimate. (If all animals failed to molt for example, modifying their numbers downward by $R^* < 1$ for their greater relative survival leaves the molting proportion unchanged and $\hat{P}_i^* = 0$.)

Direct, maximal measures of estimator uncertainty are provided by estimates of max $MSE(\hat{P}_i^*)$. Table 2 lists $\hat{P}_i^*$, $\hat{V}(\hat{P}_i^*)$, max $\hat{MSE}(\hat{P}_i^*)$, and resulting confidence intervals for P_i, all corresponding to $R_{opt}^* = 0.70$ and an assumption that $0.5 \leq R \leq 1.0$. In reference to Table 2, sampling variances were considerably higher for those size intervals in which $0.15 < \hat{P}_i^* < 0.85$. Also, as Fig. 9 had indicated, the potential for bias was much greater, again, for those size intervals in which $0.15 < \hat{P}_i^* < 0.85$. Considering sampling variance and bias simultaneously, interval estimates for P_i were fairly tight for those size intervals in which $\hat{P}_i^*$ was either >0.85 or <0.15 and not so tight otherwise (Table 2).

To summarize, high confidence may be placed in point estimates of P_i over the size ranges 106.0 to 136.0 mm and 154.00 to 166.0 mm. While the P_i estimates are less certain over the central portion of the size range, a steep decline in molting probability from near 0.90 to near 0 over the narrow range of 133 to 157 mm carapace width seems clear. Most adult female Dungeness crabs thus appear to molt annually until they reach a carapace width of about 135 mm. Thereafter, annual molting probabilities decline with increasing size until molting effectively ceases among crabs exceeding about 160 mm carapace width.

Discussion

Application of the estimators presented in this paper requires careful consideration of several explicit assumptions. These assumptions include: (1) a well-defined molting season of relatively short duration, (2) high classification accuracy, (3) a nonselective postmolting season sample (with respect to molt status and the size range of interest), and (4) a premolt-postmolt relation that is linear with an additive and normally distributed error term of constant variance. In addition, estimation of molting probabilities using postmost indicators requires that (5) the ratio (R_i) of size-specific survival probabilities through the molting season for molted and nonmolted individuals is known exactly, or is known to fall within a specifiable interval. Below we consider each of these assumptions in the context of the data for adult female Dungeness crabs, and in the broader context of general estimator application.

Analyses suggest that the first four assumptions were reasonable for the adult female Dungeness crab data from northern California. First, the molting season for adult female Dungeness crabs is well-defined and of relatively short duration (Butler 1961; Wild 1980; Hankin et al. 1989). Second, crabs were collected shortly after the molting season and could be classified with near certainty on the basis of shell condition. Third, postseason molt composition samples were collected using stationary trap gear known to be nonselective over the adult size range being considered (Diamond 1983; Diamond and Hankin 1985). Resultant molt composition was similar to that based on data of the previous year known to be nonselective with respect to molt status (Hankin et al. 1989). Finally, the stochastic model assumed to relate postmolt size to premolt size was suggested by the data (Figs. 4 and 5).

The requirement that R_i is known exactly, or is known to fall

within a specifiable interval, is an unfortunate requirement of any method for estimating molting probabilities based on postseason data. At present, estimates of R_i seem unavailable for any decapod population, but plausible interval specification for R_i does seem feasible. First, there is a definite increase in hazard associated with the molting process itself; some molting individuals will not survive the process of ecdysis. Second, a reasonable a priori assumption is that freshly molted animals with uncalcified exoskeletons are more vulnerable to predation. It therefore seems reasonable to assume that $R_i \leq 1$. We are not aware of any direct empirical evidence which supports this assumption, however, for female Dungeness crabs (or for any other decapod).

For the Dungeness crab data analyzed in this paper, specification of an interval as broad as $0.4 \leq R \leq 1.0$ into the estimation procedure sacrificed little as regards maximum uncertainty of $\{\hat{P}_i^*\}$ taken as a lot (Fig. 8). Also, the pattern of decline in size-specific molting probabilities was little influenced by choice of R^* within this interval (Fig. 9). Estimated molting probabilities were near one for small female Dungeness crabs (<135 mm carapace width) and declined precipitously until they were near zero among large female crabs (>160 mm carapace width), for all values of R^*.

Previous authors who have estimated molting probabilities from postseason data have tacitly assumed $R = 1$. In so doing, they have failed to recognize the potential impact of R_i on molting probability estimates and their uncertainty (e.g. Bennett 1974; Campbell 1983). In this regard, we emphasize that R_i need be accounted for in analyses of mark–recapture data as well as postmolt indicator data. If survival probabilities through the molting season are lower for molting animals than for nonmolting animals, then size-specific proportions of molted individuals among marked recoveries will be negatively biased (even if there are no size-selection biases in recovery data). Methods developed in this paper for incorporating the uncertainty of R_i within the estimation scheme could be adapted to mark–recapture estimation of molting probabilities as well.

Appendix B shows that the size-specific survival ratio, R_i, can in principal be estimated through comparison of preseason and postseason indicator data. Preseason estimators of molting probability do not require knowledge of R and would seem attractive if an accurate and cost-effective premolt indicator exists. However, use of molting probability estimates as a basis for description of cohort growth with age would still require consideration of possible differential survival of molting and nonmolting animals. In view of its importance for estimation of molting probabilities and subsequent description of growth in decapods, we encourage the initiation of empirical studies designed for determination of R_i.

Of potential postmolt indicators of recent molting history, only shell condition has been tested in a realistic field context. Weber and Miyahara (1962) estimated classification accuracy of at least 98.5% in their study of king crab, based on direct comparison of visual classifications with known molting records (tag recoveries). Ennis (1977) asserted that classification accuracy approached 97% for the American lobster, based on comparison of visual classifications with known molting records and serum protein concentrations. These studies indicate that the assumption of high classification accuracy can be met for at least some commercially important crustaceans, and suggest that it could be met for other crustaceans with a well-defined molting season. We emphasize, however, that classification by visual inspection of external carapace condition is inherently subjective. The level of classification accuracy achieved in practice must, to some degree, depend on the experience and training of the individual performing the classification.

Use of postmolt indicators to estimate molting probabilities requires knowledge of the premolt–postmolt relation. Hankin et al. (1989) generated a large number of molt increments by capture of female Dungeness crabs that were found in premating embraces (which indicated imminent ecdysis) with male crabs. These crabs then molted within 1–4 d in a laboratory. This method of generating molt increments for Dungeness crabs has been used previously (Butler 1961; Cleaver 1949) and may be useful for other species exhibiting this or similar premating behaviors (e.g. *Cancer pagurus*, Hartnoll 1969). Molt increment records have also been generated by inspection of burrows of newly molted animals for cast exoskeletons (Cooper 1970 — American lobster). Use of such methods for generation of molt increment data is far less common than use of mark–recapture methods, however.

The requirement for molt increment data does not necessarily diminish the potential usefulness of postmolt indicator methods for estimation of molting probabilities. Many mark–recapture studies of crustaceans have reported incomplete or equivocal findings with respect to molting probabilities (e.g. Hankin et al. 1989; Hancock and Edwards 1967; Conan and Gunderson 1979; Campbell 1983), but these same studies have often provided an adequate description of the premolt–postmolt relation. In addition, premolt–postmolt relations appear to vary little between years (Anonymous 1979; Conan and Gunderson 1979; Ennis 1972; Campbell 1983; Bennett 1974). In contrast, annual molting probabilities appear to be environmentally sensitive and may vary considerably between years (Anonymous 1979; Weber and Miyahara 1962; Campbell 1983; Aiken 1980; Kurata 1962); estimates based on a single year's collections may be misleading. Therefore, a previously established premolt–postmolt relation might be used repeatedly with annual collections of postmolt indicator data to estimate annual molting probabilities and to examine between year variation in estimates.

The estimation strategy proposed in this paper, through its formal incorporation of a plausible interval for R, allows (1) assessment of the importance of differential survival (between molting and nonmolting animals) on molting probability estimates, and (2) calculation of measures of maximum uncertainty associated with such estimates. We regard both of these features as significant improvements in methodologies used to estimate molting probabilities of decapod crustaceans.

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Appendix A. Formal Derivations of Estimators and Their Properties

Definitions

We develop estimators for size-specific molting probabilities in terms of event probabilities for an individual animal, relying primarily on basic probability relations including the definition of conditional probability, the "addition theorem" for probabilities, and Bayes theorem (Feller 1968). We use conventional notation. For example, $P(A,B|C)$ denotes the conditional probability that events A and B take place given that event C takes place.

Define the following events for an individual animal:

Event label	Definition
i	Belong to the premolt size interval i
j	Belong to the postmost size interval j
M	Molt
$\tilde{M}$	Fail to molt
S	Survive through the molting season

giving correspondences: $P_{pre,i} = P(i,M|S)$; $P_{fail,i} = P(i,\tilde{M}|S)$; $S_{i,m} = P(S|i,M)$; $S_{i,f} = P(S|i,\tilde{M})$; $P_{post,j} = P(M,j|S)$; $\pi_{ij} = P(i|M,j,S)$.

For an individual belonging to premolt size interval i, (preseason) molting probability, P_i, is, by definition of conditional probability:

$$\text{(A1)}\quad P_i = P(M|i) = \frac{P(i,M)}{P(i)} = \frac{P(i,M)}{P(i,M)+P(i,\tilde{M})}\ .$$

Again by definition of conditional probability, $P(i,M) = P(i,M,S)/P(S|i,M)$ which on division by $P(S)$ becomes $P_{pre,i}/S_{i,m}$. Similarly, $P(i,\tilde{M}) = P(i,\tilde{M},S)/P(S|i,\tilde{M})$ which on division by $P(S)$ becomes $P_{fail,i}/S_{i,f}$, thus proving equation (1). We may further partition $P_{pre,i}$ as

$$\text{(A2)}\quad P_{pre,i} = P(i,M|S) = \sum_j P(i,M,j|S)$$

$$= \sum_j P(i|M,j,S)P(M,j|S) = \sum_j \pi_{ij}P_{post,j}\ ,$$

giving equation (2).

Point Estimators

The maximum likelihood estimator for P_i and its properties are now derived under the linear premolt–postmolt model specified by relation (4).

Assume R_i known. Denote by $\mathbf{P}_{post}$ and $\mathbf{P}_{fail}$ the vectors $(P_{post,1},\ldots,P_{post,J})$ and $(P_{fail,1},\ldots,P_{fail,I})$. In consideration of equations (2), (5), and (6), let $\boldsymbol{\Theta}_1 = (\mathbf{P}_{post},\mathbf{P}_{fail})$, $\boldsymbol{\Theta}_2 = (\alpha,\beta,\sigma^2)$, $\boldsymbol{\Theta} = (\boldsymbol{\Theta}_1,\boldsymbol{\Theta}_2)$, and write $P_i = P_i(\boldsymbol{\Theta})$ to express the dependence of P_i upon $\boldsymbol{\Theta}$. The maximum likelihood estimator (mle) for $P_i(\boldsymbol{\Theta})$ is given by $P_i(\hat{\boldsymbol{\Theta}})$ where $\hat{\boldsymbol{\Theta}}$ denotes the mle for $\boldsymbol{\Theta}$. This result is a consequence of the invariance property of maximum likelihood estimators: the mle for a function of parameters is

the function evaluated at the parameter mle's (Cox and Hinkley 1974, p. 287).

Owing to the independence of the postseason molt composition sample ("sample 1") and the premolt–postmolt sample ("sample 2"), the full likelihood $L(\boldsymbol{\Theta})$ may be product factored into the two respective marginal likelihoods; $L(\boldsymbol{\Theta}) = L_1(\boldsymbol{\Theta}_1) \cdot L_2(\boldsymbol{\Theta}_2)$. Since no component of $\boldsymbol{\Theta}$ is common to both L_1 and L_2, maximization of L over $\boldsymbol{\Theta}$ is equivalent to maximizing L_1 over $\boldsymbol{\Theta}_1$ and, subsequently, L_2 over $\boldsymbol{\Theta}_2$. Thus $\hat{\boldsymbol{\Theta}} = (\hat{\boldsymbol{\Theta}}_1, \hat{\boldsymbol{\Theta}}_2)$ where $\hat{\boldsymbol{\Theta}}_1$ and $\hat{\boldsymbol{\Theta}}_2$ are the marginal mle's for $\boldsymbol{\Theta}_1$ and $\boldsymbol{\Theta}_2$. In other words, if $\hat{\boldsymbol{\Theta}}_1$ denotes the mle for $(\mathbf{P}_{post}, \mathbf{P}_{fail})$ considering sample 1 alone, and $\hat{\boldsymbol{\Theta}}_2$ denotes the mle for $(\alpha, \beta, \sigma^2)$ considering sample 2 alone, the mle for $\boldsymbol{\Theta}$ considering the whole of the data is given by $\hat{\boldsymbol{\Theta}} = (\hat{\boldsymbol{\Theta}}_1, \hat{\boldsymbol{\Theta}}_2)$.

Assuming the total (population) number of individuals greater than size $x_1 - \frac{1}{2}h$ is large relative to n_1, sample 1 is effectively from a multinomial distribution, and thus

$$(A3)\quad L_1(\boldsymbol{\Theta}_1) = \frac{n_1!}{\prod n_{post,j}! \prod n_{fail,i}!} \prod \mathbf{P}_{post,j}^{n_{post,j}} \prod \mathbf{P}_{fail,i}^{n_{fail,i}}$$

for which the sample proportions are maximum likelihood estimators (Lehmann 1983, example 6.5.7, p. 442–443):

$$(A4)\quad \hat{\mathbf{P}}_{post} = \mathbf{n}_{post}/n_1; \qquad \hat{\mathbf{P}}_{fail} = \mathbf{n}_{fail}/n_1.$$

Here $\mathbf{n}_{post}$ and $\mathbf{n}_{fail}$ denote the vectors $(n_{post,1}, \ldots, n_{post,J})$ and $(n_{fail,1}, \ldots, n_{fail,I})$, respectively.

Given the independence among the n_2 premolt–postmolt observations $\{(x_i, y_i); i = 1,2,\ldots,n_2\}$, and assuming relation (4) holds, the marginal likelihood for sample 2 may be written as

$$(A5)\quad L_2(\boldsymbol{\Theta}_2) = \prod^{n_2} f_{X,Y}(x_i, y_i) = \prod^{n_2} f_Y(y_i) f_{X|Y}(x_i|y_i)$$

$$= f_{\mathbf{Y}}(\mathbf{y}) \cdot (2\pi\sigma^2)^{-n_2/2} \exp\left(-\frac{1}{2\sigma^2} \sum^{n_2} (x_i - (\alpha + \beta y_i))^2\right),$$

$f_{\mathbf{Y}}(\mathbf{y}) = \prod^{n_2} f_Y(y_i)$. Maximum likelihood estimators are functions of sufficient statistics and in this case a sufficient statistic for $\boldsymbol{\Theta}_2$ is $(\hat{\alpha}, \hat{\beta}, \hat{\sigma}^2, \Sigma y_i, \Sigma y_i^2)$ (Cox and Hinkley 1974, example 2.27, p. 32–33) where $\hat{\alpha}$, $\hat{\beta}$, and $\hat{\sigma}^2$ are the usual mle's (given by equation (7)) for a linear model with normally distributed error of constant variance.

Finally, the mle for $\boldsymbol{\Theta}$ is therefore $\hat{\boldsymbol{\Theta}} = (\hat{\mathbf{P}}_{post}, \hat{\mathbf{P}}_{fail}, \hat{\alpha}, \hat{\beta}, \hat{\sigma}^2)$. Substitution of $\hat{\boldsymbol{\Theta}}$ for $\boldsymbol{\Theta}$ in equation (2), for each i ($i = 1,2,\ldots,I$), gives the vector mle for the I molting probabilities (denoted by $\mathbf{P}(\hat{\boldsymbol{\Theta}})$).

Consistency, Efficiency, and Asymptotic Distribution of $\mathbf{P}(\hat{\boldsymbol{\Theta}})$

Statistical properties of the estimator $\mathbf{P}(\hat{\boldsymbol{\Theta}})$ may be derived from those of $\hat{\boldsymbol{\Theta}}$ and consideration of the underlying sample structure. In particular, as noted above, the premolt–postmolt sample is independent of the molt composition sample. Also, the premolt size observations given the postmolt size vector $\mathbf{Y} = \mathbf{y}$, while independent of each other, are not identically distributed. This form of likelihood and resultant mle properties are considered by Lehmann (1983) in Theorems 6.6.1 (p. 443–444) and 6.4.1 (p. 429–435) (see also Bradley and Gart 1962). Application of these theorems to the present case show $\hat{\boldsymbol{\Theta}}$ to be asymptotically distributed as multivariate normal with expectation $\boldsymbol{\Theta}$ and variance–covariance matrix

$$(A6)\quad \boldsymbol{\Sigma} = \begin{bmatrix} \boldsymbol{\Sigma}_{11} & \boldsymbol{\Sigma}_{12} \\ \boldsymbol{\Sigma}_{21} & \boldsymbol{\Sigma}_{22} \end{bmatrix}$$

where $\boldsymbol{\Sigma}_{11}$ is the usual variance–covariance matrix for $\hat{\boldsymbol{\Theta}}_1$ (a vector of proportions based on a multinomial sample):

$$(A7)\quad \boldsymbol{\Sigma}_{11} = \begin{bmatrix} \boldsymbol{\Sigma}_{11a} & \boldsymbol{\Sigma}_{11b} \\ \boldsymbol{\Sigma}_{11c} & \boldsymbol{\Sigma}_{11d} \end{bmatrix};$$

$\boldsymbol{\Sigma}_{11a}$ is $J \times J$, $\boldsymbol{\Sigma}_{11d}$ is $I \times I$, $\boldsymbol{\Sigma}_{11b} = \boldsymbol{\Sigma}'_{11c}$ is $J \times I$; and

$$(A8)\quad [\boldsymbol{\Sigma}_{11a}]_{jj'} = \begin{cases} P_{post,j}(1 - P_{post,j})/n_1 & ; j = j' \\ -P_{post,j} P_{post,j'}/n_1 & ; j \neq j' \end{cases}$$

$$(A9)\quad [\boldsymbol{\Sigma}_{11d}]_{ii'} = \begin{cases} P_{fail,i}(1 - P_{fail,i})/n_1 & ; i = i' \\ -P_{fail,i} P_{fail,i'}/n_1 & ; i \neq i' \end{cases}$$

$$(A10)\quad [\Sigma_{11b}]_{ji} = [\Sigma_{11c}]_{ij} = -P_{post,j} P_{fail,i}/n_1;$$

Σ_{22} is the usual variance–covariance matrix for $\hat{\boldsymbol{\Theta}}_2$ (i.e. for maximum likelihood estimators of $(\alpha, \beta, \sigma^2)$ given an additive and normally distributed error term of constant variance):

$$(A11)\quad \boldsymbol{\Sigma}_{22} = \sigma^2 \begin{bmatrix} \dfrac{\Sigma y_i^2}{n_2 \Sigma (y_i - \bar{y})^2} - \dfrac{\bar{y}}{\Sigma (y_i - \bar{y})^2} & 0 \\ -\dfrac{\bar{y}}{\Sigma (y_i - \bar{y})^2} & \dfrac{1}{\Sigma (y_i - \bar{y})^2} \\ 0 & 0 \end{bmatrix} \quad 0 \quad 0 \quad \frac{2(n_2 - 2)\sigma^2}{n_2^2} \Bigg];$$

and $\boldsymbol{\Sigma}_{12} = \boldsymbol{\Sigma}'_{21} = \mathbf{0}$. $\hat{\boldsymbol{\Theta}}$ is consistent for estimating $\boldsymbol{\Theta}$ and asymptotically efficient in view of $\hat{\boldsymbol{\Theta}}_k$'s (asymptotic) variance achieving the lower bound set forth by the information inequality (Lehmann 1983, theorem 6.4.1, p. 429–435).

It follows, from the asymptotic normality of $\hat{\boldsymbol{\Theta}}$, that the mle $\mathbf{P}(\hat{\boldsymbol{\Theta}})$ is asymptotically distributed as multivariate normal (Lehmann 1983, theorem 5.1.9, p. 344). Thus, for large n_1, n_2; $\mathbf{P}(\hat{\boldsymbol{\Theta}})$ is approximately $N(\mathbf{P}(\boldsymbol{\Theta}), \mathbf{D}\boldsymbol{\Sigma}\mathbf{D}')$ where $\mathbf{D}$ is the matrix of partial derivatives:

$$(A12)\quad d_{ik} = \frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}$$

(Lehmann 1983, theorem 5.1.9, p. 344). In terms of the individual $P_i(\hat{\boldsymbol{\Theta}})$, this implies that the asymptotic variance of $P_i(\hat{\boldsymbol{\Theta}})$ is given by

$$(A13)\quad V(P_i(\hat{\boldsymbol{\Theta}})) = \sum_k \sum_{k'} \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}\right) \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_{k'}}\right) \sigma_{kk'}$$

$$= \sum_k \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}\right)^2 \sigma_k^2 + 2 \sum_k \sum_{k<k'} \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}\right) \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_{k'}}\right) \sigma_{kk'}$$

where $\sigma_{kk'}$ are the elements of $\boldsymbol{\Sigma}$ and $\sigma_k^2 = \sigma_{kk}$. The asymptotic covariance of $P_i(\hat{\boldsymbol{\Theta}})$ and $P_{i'}(\hat{\boldsymbol{\Theta}})$ is

$$(A14)\quad COV(P_i(\hat{\boldsymbol{\Theta}}), P_{i'}(\hat{\boldsymbol{\Theta}})) = \sum_k \sum_{k'} \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}\right) \left(\frac{\partial P_{i'}(\boldsymbol{\Theta})}{\partial \theta_{k'}}\right) \sigma_{kk'}.$$

Consistency and asymptotic efficiency of $\mathbf{P}(\hat{\boldsymbol{\Theta}})$ for $\mathbf{P}(\boldsymbol{\Theta})$ follow as well.

Maximum likelihood estimators for $V(P_i(\hat{\boldsymbol{\Theta}}))$ and $COV(P_i(\hat{\boldsymbol{\Theta}}), P_{i'}(\hat{\boldsymbol{\Theta}}))$ are, by the invariance property of mle's, obtained by substituting $\hat{\boldsymbol{\Theta}}$ for $\boldsymbol{\Theta}$ in (A13) and (A14) respec-

tively. We also note that the consistency of these estimators implies that estimates of $\mathbf{D\Sigma D'}$ will be consistent (Cox and Hinkley 1974, p. 293) and thus can be used in place of $\mathbf{D\Sigma D'}$ without affecting the limiting distributional result (Cox and Hinkley 1974, p. 302).

Computational Formula for the Estimator of $V(P_i(\hat{\boldsymbol{\Theta}}))$

Computation of the estimator for $V(P_i(\hat{\boldsymbol{\Theta}}))$ requires explicit formulation of the partial derivatives given in equation (A12). For the $\boldsymbol{\Theta}_1$ components:

$$\text{(A15)}\quad \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial P_{post,j}}\right) = \left(\frac{P_i(\boldsymbol{\Theta})}{P_{pre,i}}\right)(1 - P_i(\boldsymbol{\Theta}))\,\pi_{ij}\,;$$

$$\left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial P_{fail,i}}\right) = -\left(\frac{P_i(\boldsymbol{\Theta})}{P_{pre,i}}\right)R_i P_i(\boldsymbol{\Theta}).$$

The portion of $V(P_i(\hat{\boldsymbol{\Theta}}))$ arising from uncertainty associated with the postseason molt composition estimates $\hat{\boldsymbol{\Theta}}_1 = (\hat{\mathbf{P}}_{post}, \hat{\mathbf{P}}_{fail})$, is thus given by (see equation (A13))

$$\text{(A16)}\quad \left(\frac{P_i(\boldsymbol{\Theta})}{P_{pre,i}}\right)^2 C_{mult,i}$$

where

$$\text{(A17)}\quad C_{mult,i} = R_i^2 P_i(\boldsymbol{\Theta})^2 V(\hat{P}_{fail,i}) + (1 - P_i(\boldsymbol{\Theta}))^2 \sum_j \pi_{ij}^2 V(\hat{P}_{post,j}) + 2(1 - P_i(\boldsymbol{\Theta}))^2 \sum_{j<j'}\sum \pi_{ij}\pi_{ij'} COV(\hat{P}_{post,j}, \hat{P}_{post,j'}) - 2R_i P_i(\boldsymbol{\Theta})(1 - P_i(\boldsymbol{\Theta})) \sum_j \pi_{ij}\, COV(\hat{P}_{post,j}, \hat{P}_{fail,i});$$

with $V(\hat{P}_{fail,i})$ given in (A9: $i = i'$), $V(\hat{P}_{post,j})$ given in (A8: $j = j'$), $COV(\hat{P}_{post,j}, \hat{P}_{post,j'})$ given in (A8: $j \neq j'$), and $COV(\hat{P}_{post,j}, \hat{P}_{fail,i})$ given in (A10).

Similarly, for the $\boldsymbol{\Theta}_2$ components, we obtain the partial derivatives:

$$\text{(A18)}\quad \left(\frac{\partial P_i(\boldsymbol{\Theta})}{\partial \theta_k}\right) = \left(\frac{P_i(\boldsymbol{\Theta})}{P_{pre,i}}\right)(1 - P_i(\boldsymbol{\Theta})) \sum_j P_{post,j}\left(\frac{\partial \pi_{ij}}{\partial \theta_k}\right)$$

and,

$$\text{(A19)}\quad \left(\frac{\partial \pi_{ij}}{\partial \alpha}\right) = -\phi_{ij}/\sigma\,;\quad \left(\frac{\partial \pi_{ij}}{\partial \beta}\right) = -\phi_{ij} y_j/\sigma\,;$$

$$\left(\frac{\partial \pi_{ij}}{\partial \sigma^2}\right) = -(z\phi)_{ij}/2\sigma^2$$

where

$$\text{(A20)}\quad \phi_{ij} = \phi(\bar{z}_{ij}) - \phi(z_{ij}),\ \text{and}\ (z\,\phi)_{ij} = \bar{z}_{ij}\phi(\bar{z}_{ij}) - z_{ij}\phi(z_{ij}),$$

with $\phi(\cdot)$ denoting the standard normal density ($\phi(w) = (2\pi)^{-1/2} e^{-w^2/2}$) and $\bar{z}_{ij}$, z_{ij} defined by equation (6). As $(\hat{\alpha}, \hat{\beta})$ are, under the normality assumption, jointly independent of $\hat{\sigma}^2$, the portion of $V(P_i(\hat{\boldsymbol{\Theta}}))$ arising from uncertainty in the premolt–postmolt relation is given by (see equation (A13))

$$\text{(A21)}\quad \left(\frac{P_i(\boldsymbol{\Theta})}{P_{pre,i}}\right)^2 \frac{(1 - P_i(\boldsymbol{\Theta}))^2}{\sigma^2} C_{reg,i},$$

where

$$\text{(A22)}\quad C_{reg,i} = \left(\sum_j \phi_{ij} P_{post,j}\right)^2 V(\hat{\alpha}) + \left(\sum_j \phi_{ij} y_j P_{post,j}\right)^2 V(\hat{\beta}) + \frac{1}{4\sigma^2}\left(\sum_j (z\,\phi)_{ij} P_{post,j}\right)^2 V(\hat{\sigma}^2) + 2\left(\sum_j \phi_{ij} P_{post,j}\right)\left(\sum_j \phi_{ij} y_j P_{post,j}\right) COV(\hat{\alpha}, \hat{\beta})$$

with $V(\hat{\alpha})$, $V(\hat{\beta})$, $COV(\hat{\alpha}, \hat{\beta})$, $V(\hat{\sigma}^2)$ being the elements of $\boldsymbol{\Sigma}_{22}$ given in equation (A11).

An estimator for $\hat{V}(P_i(\hat{\boldsymbol{\Theta}}))$ is thus obtained by substitution of $\hat{\boldsymbol{\Theta}}$ for $\boldsymbol{\Theta}$ in equation (8).

Bias Specification

The estimator for $P_i(\boldsymbol{\Theta})$ will be biased if some value other than R_i is used in its computation. However, for a particular value, say R_i^*, all results of the previous section hold with R_i^* in place of R_i; the estimator $P_i^*(\hat{\boldsymbol{\Theta}})$ (equation (2) with R_i^* and $\hat{\boldsymbol{\Theta}}$ replacing R_i and $\boldsymbol{\Theta}$) is asymptotically normally distributed with expectation $P_i^*(\boldsymbol{\Theta})$ (equation (2) with R_i^* replacing R_i) and variance as in equation (8) (with $P_i^*(\boldsymbol{\Theta})$ and R_i^* replacing $P_i(\boldsymbol{\Theta})$ and R_i), and $P_i^*(\hat{\boldsymbol{\Theta}})$ is consistent and asymptotically efficient for $P_i^*(\boldsymbol{\Theta})$. The asymptotic bias of $P_i^*(\hat{\boldsymbol{\Theta}})$ for $P_i(\boldsymbol{\Theta})$ is defined as the expected value of $P_i^*(\hat{\boldsymbol{\Theta}})$'s limiting distribution minus $P_i(\boldsymbol{\Theta})$ and thus $B(P_i^*(\hat{\boldsymbol{\Theta}})) = P_i^*(\boldsymbol{\Theta}) - P_i(\boldsymbol{\Theta})$. Rearrangement of $P_i^*(\boldsymbol{\Theta})$ (from equation (1)) provides

$$\text{(A23)}\quad P_{fail,i} = \frac{P_{pre,i}}{R_i^*}\left(\frac{1 - P_i^*(\boldsymbol{\Theta})}{P_i^*(\boldsymbol{\Theta})}\right)$$

which, when inserted into $P_i(\boldsymbol{\Theta})$ gives

$$\text{(A24)}\quad P_i(\boldsymbol{\Theta}) = \frac{P_i^*(\boldsymbol{\Theta})}{P_i^*(\boldsymbol{\Theta}) + \dfrac{R_i}{R_i^*}(1 - P_i^*(\boldsymbol{\Theta}))}.$$

Thus $B(P_i^*(\hat{\boldsymbol{\Theta}}))$ may be expressed solely in terms of $P_i^*(\boldsymbol{\Theta})$, R_i^*, and R_i as equation (9).

Appendix B. Estimation of R_i, the Ratio of Size-Specific Survival Probabilities

Noting that $P_i(\boldsymbol{\Theta}) = P_i$, we may reformulate equation (A24) as

$$\text{(B1)}\quad R_i = R_i^*\left(\frac{(1 - P_i)/P_i}{(1 - P_i^*(\boldsymbol{\Theta}))/P_i^*(\boldsymbol{\Theta})}\right).$$

Equation (B1) provides the means for extracting size-specific estimates of R_i from direct, preseason, premolt indicator-based estimates and their postseason, postmolt indicator-based counterparts. The value of R_i^* used is, in this context, arbitrary.

Detecting Synchrony of Recruitment using Short, Autocorrelated Time Series

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Synchrony of recruitment to distinct fish stocks is difficult to detect because the available time series are generally short and autocorrelated. The recent introduction of more sophisticated statistical techniques has not been particularly helpful; several contradictory interpretations of similar data sets are discussed in the paper. To help resolve the continuing controversy surrounding the question of synchrony, we review three statistical tests of independence and determine their power using simulated data. The tests are then applied to recruitment data for six cod (*Gadus morhua*) and three haddock (*Melanogrammus aeglefinus*) stocks of the northwest Atlantic. Prior to analysis each series was first-differenced to reduce autocorrelation and hence increase statistical reliability in the results. The cod stocks are shown to fluctuate independently of the haddock stocks. There is, however, evidence of synchrony for stocks of the same species; the more widely separated cod stocks have a lower mean correlation ($\bar{r}=0.4$) than the haddock ($\bar{r}=0.6$) but both correlations are significant at the 1% level. The within-species synchrony is not due to fluctuations in our index of egg production and it appears that environmental forcing is probably important.

Il est difficile de détecter le synchronisme du recrutement pour différencier les stocks de poissons parce que les séries chronologiques dont on dispose sont généralement courtes et en autocorrélation. Les techniques statistiques plus perfectionnées récemment mises au point n'ont pas été particulièrement utiles à ce point de vue; dans l'Introduction, il est question des interprétations contradictoires qu'on fait de groupes de données semblables. En vue régler la controverse qui entoure toujours la question du synchronisme, nous nous sommes penchés sur trois tests d'indépendance statistiques dont nous avons évalué la puissance au moyen de données simulées. Nous les avons ensuite appliqués à des données sur le recrutement de six stocks de morue (*Gadus morhua*) et de trois stocks d'aiglefin du nord-ouest de l'Atlantique (*Melanogrammus aeglefinus*). Avant l'analyse, chaque série a fait l'objet d'une première différenciation, ce qui réduit le facteur d'autocorrélation et dès lors, donne plus de fiabilité statistique aux résultats. Nous avons constaté que les stocks de morue fluctuent indépendamment des stocks d'aiglefin. Cependant, nous avons noté des signes de synchronisme entre les stocks de même espèce; pour les stocks de morue, plus éloignés, la corrélation moyenne est plus faible ($\bar{r}=0,4$) que pour l'aiglefin ($\bar{r}=0,6$), mais dans les deux cas, la corrélation est significative au seuil de 1 %. Par ailleurs, le synchronisme dénoté entre les stocks de même espèce n'est pas dû à la fluctuation de l'indice de ponte et il semble probable que le forçage environnemental soit important.

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Given that recruitment to widely separated stocks varies synchronously, some fisheries biologists would argue that environmental forcing is important. There is, however, a major difficulty with this argument: how does one show convincingly, with the short (~20 yr), autocorrelated time series typically available, that recruitment does indeed vary synchronously.

The first attempts to determine the spatial scale of recruitment variability were essentially qualitative and the results did not lead to a consensus. For example, Templeman (1972) examined 18 cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks of the North Atlantic and claimed "year-class success in adjacent or even distant stocks of several species have patterns of relationship too consistent to be due to chance. . .". On the other hand, Dragesund (1971) examined the year-class strength of several North Atlantic species, including cod and haddock, and concluded no co-variation existed between stocks of the same species.

Over the last 10 yr, more sophisticated statistical techniques have been applied to the problem of synchrony. Surprisingly, the results are again somewhat inconclusive. For example Garrod and Colebrook (1978) used correlation and principal component analysis and found that ". . .similar variation in planktonic and fish communities are contemporary and on a geographical scale which suggests a common origin in Pan-Atlantic environmental effects rather than strictly localized phenomena." Shepherd et al. (1984) subsequently applied Bartlett's sphericity test to Garrod and Colebrook's correlation matrix and could not reject the null hypothesis that the stocks fluctuate independently.

Koslow (1984) also used principal component analysis in a study of recruitment variability in the northwest Atlantic. Large-scale patterns were again found, this time spanning the region from west Greenland to Georges Bank, and Koslow inferred that ". . .large-scale physical forcing, rather than local biological interactions, predominantly regulates recruitment to north-

TABLE 1. Data availability and sources. The years covered by virtual population analysis (VPA) are listed in the third column. Recruitment (R), obtained from the first row of the numbers-at-age matrix, was lagged back to the year of spawning. (Cod 1, 3NO, 3Ps, and 4TVn were lagged 3 yr; Cod 2J3KL was lagged 4 yr; the rest were lagged 1 yr.) The spans of the analysed recruitment time series are listed in the fourth column followed by egg production (E). The last column gives the data sources. NAFO denotes North Atlantic Fisheries Organization and CAFSAC denotes Canadian Atlantic Fisheries Scientific Advisory Council.

NAFO region	Area	VPA	R	E	Source
Cod					
1	West Greenland	1965–82	1962–75	1965–75	NAFO Scr.Doc.82/vi/50
2J3KL	Labrador	1962–81	1958–75	1962–75	NAFO Scr.Doc.82/ix/111
3NO	Grand Banks	1959–81	1956–75	1959–75	NAFO Scr.Doc.82/vi/57
3Ps	South Newfoundland	1959–80	1956–75	1959–75	CAFSAC Res.Doc.81/39
4TVn	Gulf of St. Lawrence	1950–81	1950–75	1950–75	CAFSAC Res.Doc.81./41
4VsW	Sable Island	1958–81	1957–75	1958–75	CAFSAC Res.Doc.82/40
Haddock					
4VW	Sable Island	1960–79	1959–75	1960–75	CAFSAC Res.Doc.80/61
4X	Browns Bank	1962–80	1961–75	1962–75	CAFSAC Res.Doc.81/24
5Z	Georges Bank	1931–78	1950–75	1949–75	J. Northw. Atl. Fish. Sci. 1982, 3:1–27.

west Atlantic fisheries." However Cohen et al. (1986) have recently suggested that Koslow's patterns "...were due to his methods and not actual large scale correlations".

The difficulty in defining patterns in recruitment variability stems from the basic data; recruitment time series are generally short and autocorrelated and the synchronous signal, if it exists, is weak. It follows that considerable care must be taken in the selection and application of statistical techniques. In this paper we compare the effectiveness of three tests of independence. The tests are first described and compared using simulated data. Cod and haddock recruitment data for the northwest Atlantic are then first-differenced, to reduce autocorrelation, and then tested for independence. The results suggest that synchrony does indeed occur between stocks of the same species and that the environment, to some degree, regulates recruitment.

Data

Time series of recruitment (R) have been obtained for the six cod and three haddock stocks of the northwest Atlantic listed in Table 1. (The stock designations correspond to North Atlantic Fisheries Organization management divisions and are described, for example, by Koslow et al. (1987).) The data were derived from published virtual population analyses and are identical to those used, and plotted, by Koslow (1984) and Cohen et al. (1986). The recruitment series are continuous but of different lengths; the shortest is 14 yr (cod 1) and the longest are 26 yr (cod 4TVn, haddock 5Z). Further details on the recruitment data are given in Table 1.

Time series of annual egg production (E) for each of the nine stocks have also been calculated in order to assess its effect on recruitment. Egg production for a given stock and year (t) has been estimated from

$$(1)\quad E(t) = \frac{1}{2}\sum_{a\geq 1} T(t,a)F(a)M(a),$$

where $T(t,a)$ is the total number of fish of age a in year t, $F(a)$ is the fecundity, $M(a)$ is the female maturity ogive, and we have assumed a sex ratio of 0.5. The number of fish at age was obtained from the same sources as the recruits. The fecundity for all stocks was assumed to be proportional to a^2. (The proportionality factor does not affect the subsequent analysis of log-transformed data. This functional form for F is a compromise based upon published fecundity–age relationships listed in Table 2). A single female maturity ogive was also used for all stocks:

$$(2)\quad M(a) = \begin{cases} 0 & 1\leq a\leq 2 \\ \dfrac{a-2}{4} & 2\leq a\leq 6 \\ 1 & 6\leq a \end{cases}$$

This is again a simplification based on many published maturity ogives (Fleming 1960; Pinhorn 1969; Beacham 1983a,b; Clark 1959; Kohler 1959; and Clark et al. 1982). We determined the effect on $E(t)$ of shifting the age of 50% maturity through time. The effect was small and equation (2) appears to be a reasonable compromise.

The recruitment and egg production estimates were next combined to form a survival index, R/E, and then the time series of R and R/E were log-transformed. There is a compelling statistical reason for the transformation: the frequency distribution of recruitment is approximately log-normal (e.g. Hennemuth et al. 1980) and so log-transforming allows us to take advantage of the vast array of statistical techniques that assume normality (Shepherd et al. 1984, provide further discussion of the statistical advantages of this transformation.)

How do we interpret variations in log R and log R/E? We give below a simple interpretation based on the stock–recruit model of Beverton and Holt (1957). Let $N(t)$ denote the number of individuals in a given cohort at some time (t) in the early stages of its life history. According to the Beverton–Holt model

$$(3)\quad \frac{dN}{dt} = -(\mu_1 + \mu_2 N)N,$$

where $\mu_1(t)$ and $\mu_2(t)$ are the instantaneous coefficients of density-independent and density-dependent mortality, respectively. The solution is

$$(4)\quad N(t) = \frac{E\beta(t)}{1+\alpha(t)E}$$

where E is the initial number of eggs ($N=E$ at $t=0$),

$$(5)\quad \beta(t) = \exp\left[-\int_0^t \mu_1 dt'\right],$$

and

TABLE 2. Summary of published fecundity (F) relationships as a function of age (a) for North Atlantic cod and haddock.

	Fecundity exponent, γ, where $F = ca^{\gamma}$	Age range	Source
Cod			
2J3KL, 3NO	1.95	6–26	May (1967)
Haddock			
Grand Banks	2.005	4–15	Hodder (1963)
North Sea	1.88	2–8	Alekseyeva and Tormosova (1980)

$$(6)\quad \alpha(t) = \int_0^t \beta\mu_2 dt'.$$

Let R denote the number of recruits entering the fishery at $t = T$. From equation (4)

$$(7)\quad R = \frac{E\beta(T)}{1+\alpha(T)E}$$

Equation (7) defines the well known Beverton–Holt stock–recruit relationship. We note here that there are two limits of interest.

If the egg production in a given year is high, in the sense that $\alpha(T)E \gg 1$, then equation (7) can be approximated by

$$(8)\quad R = \frac{\beta(T)}{\alpha(T)}$$

and hence, on taking natural logarithms,

$$(9)\quad \log R = -\int_0^T \mu_1 dt - \log \alpha(T).$$

In this limit, recruitment in a given year is independent of egg production and depends, in a complicated way, on both density-dependent and density-independent mortality coefficients during the whole prerecruit stage.

If egg production in a given year is low, in the sense that $\alpha(T)E \ll 1$, then equation (7) can be approximated by

$$(10)\quad R = E\beta(T)$$

and hence

$$(11)\quad \log(R/E) = -\int_0^T \mu_1 dt.$$

In this limit recruitment is proportional to both egg production and the density-independent mortality coefficient integrated over the whole prerecruit period.

In the absence of reliable estimates of μ_1 and μ_2, or indeed convincing empirical evidence that equation (3) is the appropriate model, it is not possible to determine a priori which limit applies in this study and thus which variable to use, log R or log R/E. We have therefore analysed both variables in our search for synchrony.

Statistical Methods

A major difficulty with the statistical analysis of recruitment data is that the fluctuations from year to year are dependent. Consider, for example, the changes in recruitment to cod 3NO shown in Fig. 1. This time series is dominated by a slow decline from 1963 to 1972. Note that there is a similar trend in recruitment to cod 4VsW; the correlation between log R for cod 3NO and cod 4VsW is, in fact, equal to 0.68. However the statistical significance of this correlation is not high because both records are dominated by low-frequency variations.

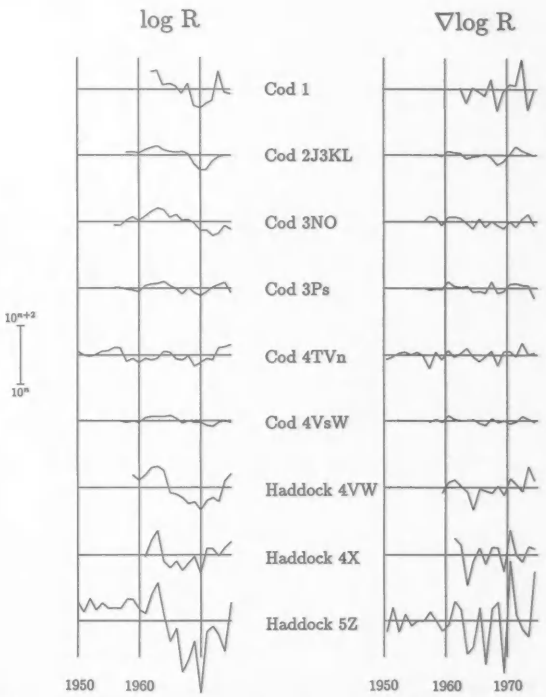

FIG. 1. Plots of log-transformed recruitment (log R) and first-differenced log-transformed recruitment (∇ log R) as a function of time for six cod and three haddock stocks of the northwest Atlantic. The mean of each log R series was removed before plotting. The scale for changes in log R and ∇ log R is shown on the left hand side of the figure.

There appear to be two ways to proceed. We could allow, in some way, for the autocorrelation within a series when assessing the statistical significance of the correlation between series. Alternatively we could attempt to remove the autocorrelation by transforming the data and then use critical levels based on the assumption of serial independence. Following the lead of Cohen et al. (1986) we have adopted the latter approach and reduced the autocorrelation by "first-differencing" the log R and log R/E data. It should be stressed that this a somewhat subjective choice and we may be removing an important, and perhaps synchronous, component of recruitment variability. On the other hand first-differencing is straightforward and will

reduce spurious trends in the recruitment data that may result from the virtual population analysis (e.g. Bradford and Peterman 1989).

First-Differencing and Serial Independence

Suppose we have a time series of length n:

$$x_1, x_2, x_3, \ldots x_n.$$

In the present context x_i could correspond to log R or log R/E for the ith year. First-differencing leads to a new series of length $n-1$:

$$x_2 - x_1,\ x_3 - x_2, \ldots x_n - x_{n-1}.$$

Following Box and Jenkins (1976) we denote the first-differenced time series by

$$(12) \quad \nabla x_i = x_i - x_{i-1} \quad i = 2, n.$$

To illustrate the effect of first-differencing on a linear trend assume

$$(13) \quad x_i = a_0 + a_1 i \quad i = 1, n$$

where a_0 and a_1 are constants. On first-differencing

$$\nabla x_i = a_0 + a_1 i - [a_0 + a_1(i-1)]$$

i.e.

$$(14) \quad \nabla x_i = a_1, \qquad i = 2, n.$$

Thus first-differencing removes completely a linear trend from the series. To illustrate the effect of first-differencing on a sinusoid assume

$$(15) \quad x_i = \sin(\omega i + \phi) \qquad i = 1, n$$

where ω, ϕ are the (constant) angular frequency and phase respectively and we have assumed a sampling interval of unity. On first-differencing

$$\nabla x_i = \sin(\omega i + \phi) - \sin[\omega(i-1) + \phi]$$

i.e.

$$(16) \quad \nabla x_i = 2 \sin\left(\frac{\omega}{2}\right) \sin\left[\omega\left(i - \frac{1}{2}\right) + \phi + \frac{\pi}{2}\right], \quad i = 2, n.$$

Thus first-differencing changes the phase of the sinusoid by $(\pi - \omega)/2$ and the amplitude by the factor $2\sin(\omega/2)$. For low frequency sinusoids ($\omega \ll 1$), $2\sin\omega/2 \approx \omega$ and the amplitude of the first-differenced sinusoid reduces proportionally with ω. For example assume the period of the sinusoid is 20 yr. It follows that $\omega = 2\pi/20$ and first-differencing reduces the amplitude of the sinusoid by a factor of $2\sin(\omega/2) \approx \pi/10$. If, on the other hand, the period of the sinusoid is equal to 4 yr then $2\sin(\omega/2) = \sqrt{2}$ and so this high-frequency sinusoid is amplified by about 40% on first-differencing. In summary, first-differencing corresponds to "high-pass filtering" the time series; it "passes" high frequency variations and attenuates those with low-frequencies. This effect is clearly evident in Fig. 1 which shows the log R series both before and after first-differencing.

Each of the $\nabla \log R$ and $\nabla \log R/E$ series has been checked for serial independence using a nonparametric test based on the distribution of phase lengths (i.e. the time between extrema). The test was proposed by Wallis and Moore (1941) and is discussed, and compared with other tests, by Kendall (1976).

Normality

All of the tests of independence described below require that the data be normally distributed. We checked each series of $\nabla \log R$ and $\nabla \log R/E$ for normality by calculating the correlation between the ordered values and their normal scores; if the correlation fell below a known critical value the null hypothesis of normality was rejected. (This well known test is described in detail, for example, by Cryer 1986.)

Interspecies Dependence

The greatest eigenvalue criterion (Morrison 1976) was used to test the hypothesis that cod recruitment fluctuates independently of haddock recruitment. The series, each of length n, are first split into the two species groupings with p_1 and p_2 series in each group. (In the present context $p_1 = 6$, $p_2 = 3$ and $n = 13$ is the number of years of data in common.) The sample correlation matrices of cod–cod (S_{11}), haddock–haddock (S_{22}) and cod–haddock (S_{12}) interactions are formed and the greatest eigenvalue of $S_{11}^{-1} S_{12} S_{22}^{-1} S_{12}'$ is calculated (where prime denotes transpose). The test involves a comparison of this eigenvalue against a calculable critical value which depends on p_1, p_2, n and the significance level of the test. The greatest eigenvalue can be interpreted as the maximum squared correlation which can be attained between any linear combination of the cod with any linear combination of the haddock series (see Morrison 1976, for further discussion).

Intraspecies Dependence

We will now examine three tests of independence that will be used to detect synchrony of recruitment to stocks of the same species. The power of each test will be assessed using the following Monte Carlo approach. Suppose that we require the power of a particular test given p recruitment series of length n. (In the present context p will be three or six, the number of cod and haddock series, and n will be the length of the common period.) First we assume that the null hypothesis of independence is true and simulate many blocks of $n \times p$ recruitment data according to the rule

$$(17) \quad x_{ij} = \epsilon_{ij} \qquad i = 1, n \quad j = 1, p$$

where the ϵ_{ij} are independent and normally distributed with unit variance and zero mean, i.e. $\epsilon_{ij} \sim N(0,1)$. If the test is to be applied at the 0.05 significance level we choose a critical value such that the proportion of blocks for which synchrony is falsely claimed is 0.05, i.e. we choose the critical value such that the probability of making a Type I error is 0.05. The next step is to determine the power of the test to detect a genuine synchronous signal. To make a quantitative comparison of the power of the three tests we have assumed that the synchronous component takes on a particularly simple form: it is of equal amplitude and phase in each of the p series. Thus we simulated many blocks of $n \times p$ recruitment data according to the rule

$$(18) \quad x_{ij} = \alpha \epsilon_i + \epsilon_{ij} \qquad i = 1, n \qquad j = 1, p,$$

where $\epsilon_i, \epsilon_{ij} \sim N(0,1)$ and independent, as in equation (17). The strength of the synchronous component ($\alpha \epsilon_i$) is measured by the constant α. Note that as n increases the sample correlation between any pair of series approaches the (population) correlation

(19) $$\rho = \frac{\alpha^2}{1+\alpha^2}$$

Thus if we fix ρ at some level we can determine α from equation (19) and then generate many blocks of $n \times p$ blocks of data according to equation (18). We can then apply the test to these blocks and calculate its power, i.e. the proportion of blocks for which the test correctly detects synchrony.

The power of three tests is compared below. It should be emphasized that we are comparing the power to detect a particularly simple form of synchrony. It did not seem worthwhile assuming a more complicated form of synchrony, such as ρ a function of distance between stocks, at this stage because we simply do not have a clear idea of the mechanisms (if any) responsible for synchrony. The following comparison should therefore be viewed as illustrative, rather than definitive.

i) Barlett's statistic (B)

Let S denote the $p \times p$ sample correlation matrix calculated from p recruitment series each of length n. Bartlett's statistic is given by

(20) $$B = -\left[n - \frac{2p+11}{6}\right] \log|S|,$$

where $|S|$ denotes the determinant of S. Bartlett has shown that, for large n, the distribution of B can be approximated by a chi-squared distribution with $p(p-1)/2$ degrees of freedom and this allows critical values for B to be readily obtained. For the present case of small n, the critical value was determined by the similation process outlined above with $\rho = 0$. The test rule is to reject the null hypothesis of independence if the observed value of B exceeds the critical value.

The power of this test has been estimated for $p = 6$, $n = 13$ and values of ρ from 0.05 to 1. (The choice of p and n matches the number and common length of first-differenced cod series.) More specifically we first selected a value of ρ and calculated α from equation (19). We then simulated 1000 blocks of $n \times p$ data according to equation (18) and determined the proportion of blocks, $\pi(\rho)$, for which the null hypothesis of independence was rejected. For nonzero ρ, $\pi(\rho)$ is the probability that the test rule will correctly detect synchrony.

A plot of $\pi(\rho)$ against ρ is shown in Fig. 2. The significance level of the test was chosen to be 0.05, i.e. the proportion of blocks for which the test rule incorrectly detects synchrony with $\rho = 0$ is 0.05. Hence $\pi(0) = 0.05$. As ρ increases the power of the test to detect the underlying synchrony increases. For example when $\rho = 0.4$ we will correctly detect synchrony in about 60% of all cases using this test rule.

(ii) Largest eigenvalue of the correlation matrix (λ_1)

Principal component analysis is becoming an increasingly popular technique for detecting large-scale patterns in recruitment (e.g. Garrod and Colebrook 1978; Koslow 1984; Shepherd et al. 1984). The analysis is usually based on time series which have been standardized to unit variance or, equivalently, the sample correlation matrix S. The quantity λ_1/p is that proportion of the total standardized variance (equal to p) that can be accounted for by the first principal component. The test rule is to reject the null hypothesis of independence if λ_1/p exceeds a critical value which can be readily estimated from Monte Carlo simulations with $\rho = 0$.

The power of this test rule is shown in Fig. 2. Clearly λ_1/p is a somewhat more reliable indicator of our simple form of synchrony. For example if we fix the strength of the synchronous signal such that $\rho = 0.4$ this test rule will correctly detect synchrony in 80% of all cases compared to 60% for a test rule based on B.

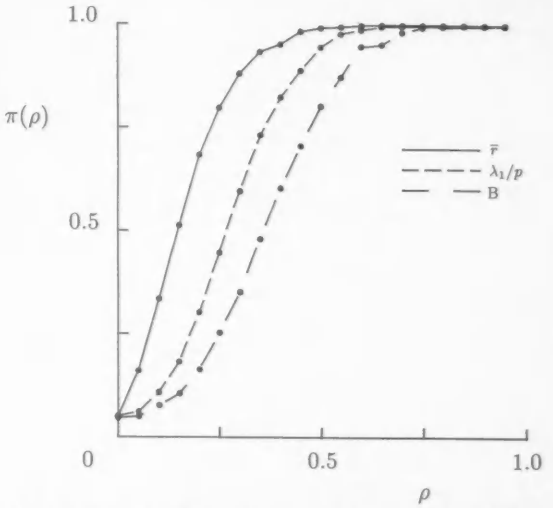

FIG. 2. Power of three tests to detect a synchronous signal, of the form specified by equation (18), in six time series, each of length 13. The strength of the synchronous component, relative to the noise, is given by ρ. If $\rho = 0$ there is no synchronous component; if $\rho = 1$ the synchronous component completely dominates the noise. The probability of correctly detecting a synchronous component for nonzero ρ is denoted by $\pi(\rho)$. This probability, and the critical value of the test statistic, have been estimated from Monte Carlo simulations. For each ρ shown, 1000 blocks of 13×6 normal random numbers with a synchronous component were generated. $\pi(\rho)$ is the proportion of blocks for which each test of independence correctly rejected the null hypothesis of independence. The random numbers were generated using the IMSL routine RNNOF.

(iii) Mean correlation ($\bar{r}$)

The final test rule is based on the arithmetic mean of the off-diagonal elements of S. If the mean correlation, $\bar{r}$, is high enough we reject the null hypothesis of independence. As before, we can easily estimate the critical value of $\bar{r}$ from Monte Carlo simulations with $\rho = 0$. The power of this test rule is shown in Fig. 2; for a synchronous signal of strength $\rho = 0.4$ it will correctly detect synchrony in 95% of all cases.

In summary the most effective statistic for detecting our large-scale synchronous signal is $\bar{r}$. However it is clear that it would not be as effective if the sign of the synchronous component differed between stocks; this would lead to correlations of opposite signs which would tend to cancel when forming $\bar{r}$. The largest eigenvalue test does not suffer from this deficiency. A further advantage of a λ_1-based test is that the eigenvector associated with λ_1 describes the spatial pattern of the synchronous component. With reference to the relatively poor performance of Bartlett's statistic it should be remembered that we have assumed a particularly simple form of synchrony; presumably it would be straightforward to construct more exotic forms of synchrony for which Bartlett's statistic performed best. However, the point of the simulations was to highlight the difficulty in detecting large-scale recruitment patterns with the short, noisy time series that are usually available for analysis.

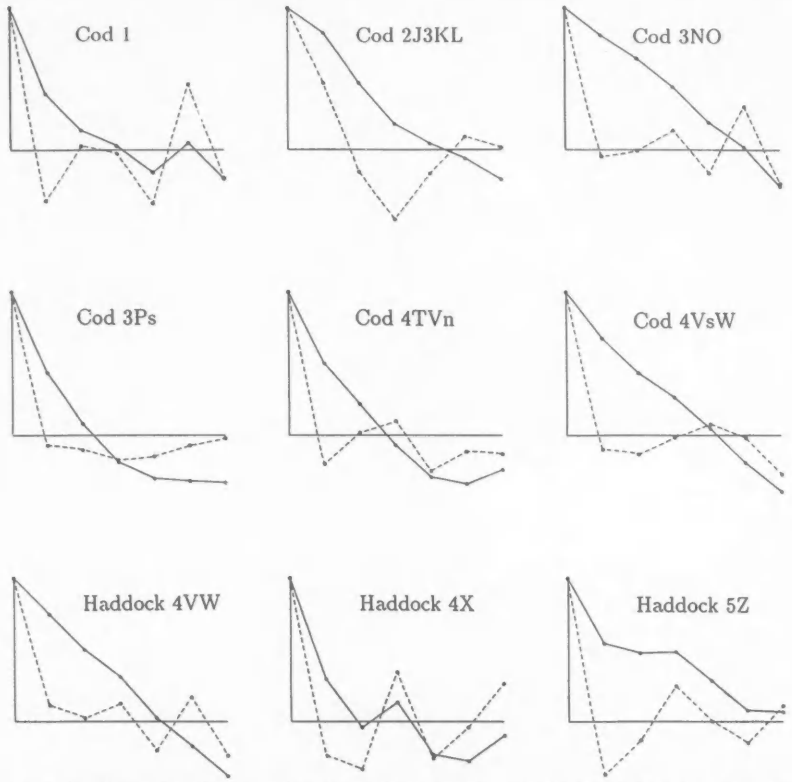

FIG. 3. Autocorrelation of log-transformed recruitment ($\log R$ = solid line) and first-differenced recruitment ($\nabla \log R$ = dashed line) as a function of lag in years. All available data for each series were used (Table 1). The autocorrelations were calculated using the IMSL routine ACF.

Northwest Atlantic Recruitment

The fluctuations of log R from year to year are not independent (Fig. 1). The effect of first-differencing is clearly evident in the accompanying plots of $\nabla \log R$ (Fig. 1) and their autocorrelation functions (Fig. 3). On applying the phase-length test of serial dependence we found that only one first-difference series, cod 2J3KL, does not appear random at the 0.05 significance level.

A similar analysis was performed on the log R/E and $\nabla \log R/E$ series. First-differencing strongly reduced the autocorrelation and the only series which could not be considered random was, again, cod 2J3KL.

The $\nabla \log R$ and $\nabla \log R/E$ series were checked separately for normality using the normal scores correlation test run at the 0.05 significance level. All series were consistent with the assumption of normality as required by the following tests of independence.

Does cod recruitment fluctuate independently of haddock recruitment in the northwest Atlantic? Koslow (1984) and Koslow et al. (1987) reported weak, but significant, correlations between these two species. Cohen et al. (1986) have subsequently shown that first-differencing the log R series prior to analysis lowers the overall correlation between species. But is there still statistical evidence that (first-differenced) cod and haddock recruitment covary? We applied the greatest eigenvalue test to $\nabla \log R$ for the common period 1962–75 and found no evidence of synchrony. Presumably the cod–haddock correlations reported by Koslow (1984) and Koslow et al. (1987) result from the low-frequency variations in log R which are strongly attenuated by first-differencing.

TABLE 3. Tests of dependence of recruitment to stocks of the same species in the northwest Atlantic, 1962–75. Each recruitment series was log-transformed and first-differenced prior to analysis. The three test statistics are as follows: Bartlett's statistic (B); the proportion of standardised variance accounted for by the first principal component (λ_1/p); and the arithmetic mean of the stock–stock correlations. The second and third columns list the values of those three statistics for the six cod and three haddock stocks, respectively. Significance levels for the three test statistics were based on Monte Carlo simulations with $\rho = 0$, as outlined in the text.

Test statistic	Cod	Haddock
B	18.6	14.1*
λ_1/p	0.48*	0.73**
$\bar{r}$	0.37**	0.59**

*Significant at 0.05 level.
**Significant at 0.005 level.

Does recruitment to stocks of the same species fluctuate together? The first-differenced haddock series provide strong evidence for synchrony (Table 3). For example the average correlation between the $\nabla \log R$ haddock series is $\bar{r} = 0.59$. This is significant at the 0.005 level. Tests based on B and λ_1/p also indicate synchrony, significant at the 0.05 level. Note that

adjusting recruitment for changes in egg production did not affect the synchrony; the values of $\bar{r}$, λ_1/p and B based on $\nabla \log R/E$ were still significant at the 0.05 level.

The cod series also show evidence of synchrony although it is weaker than that found for the haddock (Table 3). For example the average correlation between the $\nabla \log R$ cod series is only 0.37 in contrast to $\bar{r}=0.59$ for haddock. Note that we did not detect synchrony at the 0.05 significance level using Bartlett's test statistic. This apparent contradiction should not be surprising given the poor performance of B in tests based on simulated data with a weak synchronous component (Fig. 2). A similar analysis of $\nabla \log R/E$ showed that the weak synchrony of cod recruitment is not due to changes in egg production.

What is the spatial form of the synchrony? We tested for equality of the true haddock–haddock correlations using the Lawley test outlined by Morrison (1976, p. 269). It was not possible to reject the null hypothesis that the three haddock–haddock correlations are in fact equal and we accept $\bar{r}=0.6$ as an estimate of the correlation between any pair of haddock stocks. On the basis of the Lawley test we also accept that the true cod–cod correlations are equal at the 0.05 significance level and estimate the correlation between any pair of cod stocks by $\bar{r}=0.4$. Thus the spatial pattern of synchronous recruitment for both cod and haddock is consistent with the simple form assumed for the Monte Carlo simulations. We found no evidence that distance between stocks affects the correlation.

The argument outlined in the Introduction would suggest that recruitment to the widely separated cod stocks is regulated, to some degree, by the environment. Koslow et al. (1987) correlated $\log R$ with selected environmental indices for the northwest Atlantic and, although some significant correlations were found, they were unable to obtain a clear understanding of the underlying mechanisms. The difficulty stems in part from autocorrelation in both data sets which results in fewer degrees of freedom than data points and hence an increased probability of spuriously high sample correlations. A more robust approach may be to correlate recruitment and environmental indices after first-differencing; this will reduce the autocorrelation and increase both degrees of freedom and our confidence in the cross-correlations. However, given that synchrony is weakened by first-differencing, it is natural to ask if it is still be possible to detect an environmentally-induced response in the short $\nabla \log R$ or $\nabla \log R/E$ series. This question is probably best answered by a simple example.

Suppose that recruitment to the six cod stocks is due to a common environmental signal and a random component, i.e. let us adopt the model used for the Monte Carlo simulations

$$x_{ij}=\alpha\epsilon_i+\epsilon_{ij} \qquad i=1,n \qquad j=1,6$$

where x_{ij} is $\nabla \log R$ for the jth stock in year i, $\alpha\epsilon_i$ is the common environmental signal and ϵ_{ij} is the random component. As noted in the previous section, the correlation between any pair of recruitment series increases with the strength of the environmental signal: for large n it is approximately given by $\rho=\alpha^2/(1+\alpha^2)$. It is straightforward to show that the correlation between the environmental signal and any recruitment series approaches $\sqrt{\rho}$ as n increases. Let us suppose that $\rho=0.4$ in accord with our analysis of the cod data. Then, in the unlikely event that we were given the environmental signal, its correlation with any recruitment series would be $\sqrt{\rho}=0.63$. Unfortunately the typical length of the cod series is only 20 yr; even given $\alpha\epsilon_i$, this is barely long enough to detect an environmental influence at the 0.05 significance level.

There is a straightforward way to increase the signal-to-noise ratio of the large-scale environment component: simply average the six cod series. It is easily shown that the correlation between $\alpha\epsilon_i$ and $\Sigma_{j=1}^{6} x_{ij}/6$ approaches $[6\rho/1+5\rho]^{1/2}$ as n increases. For $\rho=0.4$, $[6\rho/1+5\rho]^{1/2}=0.89$. This would certainly be detectable with 20 yr of recruitment data and clearly illustrates the advantage of combining recruitment series.

To conclude this section we have taken the above ideas one step further and averaged our $\log R$ cod series over their common period, 1962–75. We have also obtained from J. A. Koslow the second principal component of annual air pressure over the North Atlantic. This environmental index was shown to be correlated with fluctuations in cod recruitment by Koslow et al. (1987). Indeed the correlation between our averaged $\log R$ series and the environmental index is -0.75. It is difficult, however, to assess the statistical significance of this correlation because of the autocorrelation. We could attempt to calculate the reduction in degrees of freedom due to autocorrelation in the manner proposed by Garrett and Toulany (1981) and implemented by Koslow et al. (1987). Alternatively we could first-difference the recruitment and reduce the autocorrelation. Taking the latter approach we find that the correlation between the mean $\nabla \log R$ and the environmental series drops to -0.31 which is not significant at the 5% level. Thus we are left with little confidence in a relationship, empirical or otherwise, between cod recruitment and this particular environmental index unless, of course, the relationship holds only for those low frequency variations which have been removed by first-differencing.

Discussion

Recruitment time series are usually short and autocorrelated. The cod and haddock data analysed here are no exception; the median length of the nine series is only 19 yr and the autocorrelation of log-transformed recruitment at a lag of 1 yr is typically 0.6. Such data are difficult to analyse. In particular it is difficult to assess the statistical significance of correlations between these series and hence detect spatial patterns of recruitment variability. Koslow et al. (1987) used the somewhat ad hoc procedure suggested by Garrett and Toulany (1981) to test the significance of correlations between their northwest Atlantic recruitment series. However, as noted by Cohen et al. (1986), the procedure of Garrett and Toulany assumes that the time series are stationary and that assumption is difficult to justify with short, autocorrelated recruitment series. More importantly Garrett and Toulany's procedure requires an estimate of the autocorrelation of the cross-product series and this is difficult to obtain with short records.

We have tackled the autocorrelation problem in a very direct way: we have removed it by first-differencing our recruitment series. Effectively we have applied a "high-pass" filter, attenuating low-frequency variations and "passing" those at high frequencies. The advantage of this approach is that we could use standard statistical theory to test the statistical significance of our results. The obvious disadvantage is that we may remove an important, and indeed synchronous, component of the recruitment variability. However it is possible that the assumptions made in a virtual population analysis can cause trends in recruitment series (e.g. Bradford and Peterman 1989) and, since these spurious trends cannot be separated from real low-frequency variations, it is perhaps best to remove them both by first-differencing.

The power of three tests of independence was estimated using Monte Carlo techniques. Essentially we estimated their ability to detect a common signal buried in six short, noisy time series each of length 13. If the synchronous component was much stronger than the noise then, not surprisingly, all three tests had no difficulty in detecting it. However, if the strength of the synchronous component was reduced to a more typical level ($\rho = 0.4$), substantial differences were found in the performance of the tests. For example, we expect the test based on Bartlett's statistic (B) to fail to detect our simple form of synchrony in 40% of all applications. This is unfortunate because the distribution theory associated with B is well developed (e.g. Morrison 1976) and the test is straightforward to apply. Shepherd et al. (1984) applied this test to the correlation matrix of Garrod and Colebrook (1978) and found that they could not reject the null hypothesis that all the recruitment series were uncorrelated. Garrod and Colebrook (1978), on the other hand, claimed that some of the correlations were indeed significant and that the matrix contained evidence of multispecies associations which spanned large geographic areas. Given the poor performance of B in the present simulations, it is perhaps not surprising that opposite conclusions can be drawn from the same data set.

We have applied the three tests of independence to our first-differenced cod and haddock series. We conclude that recruitment to stocks of the same species does indeed vary synchronously in the northwest Atlantic. This confirms the results of Koslow (1984) who analysed the same basic data but without first-differencing. However we found no evidence for synchrony between species; presumably the significant cod-haddock correlations found by Koslow (1984) are due to low-frequency fluctuations which have been removed by first-differencing. It is important to note however that the within-species synchrony is weak. For example, our estimate of the mean correlation between the six cod series is only 0.4. If we assume that this correlation is due to a common environmental signal, then only 40% of the recruitment variance is due to large-scale forcing by the environment. Thus we conclude that most of the variance in first-differenced cod recruitment is due to small spatial scale variability and noise in the data.

We found no significant correlations between the first-differenced series of log-transformed recruitment and egg production. In the context of the Beverton–Holt stock–recruit model it would appear that the high egg production limit, equation (8), applies and that both density-dependent and density-independent mortality coefficients, rather than E, will determine recruitment. This will obviously complicate any attempt to identify the factors, environmental or otherwise, affecting recruitment.

An obvious way to increase the signal-to-noise ratio of any environmental effect is to average the recruitment series in some way, perhaps using principal component analysis to determine the appropriate weighting factors (Shepherd et al. 1984). This procedure, coupled with first-differencing to reduce autocorrelation and increase degrees of freedom, should lead to more robust correlations between recruitment and the environment.

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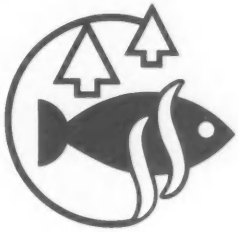

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